# Taxonomic studies of Diospyros (Ebenaceae) from the Malagasy region. VI. New species of large trees from Madagascar

George E. Schatz, Porter P. Lowry II, Hasina N. Rakouth & Richard Randrianaivo

### **Abstract**

SCHATZ, G.E., P.P. LOWRY II, H.N. RAKOUTH & R. RANDRIANAIVO (2021). Taxonomic studies of Diospyros (Ebenaceae) from the Malagasy region. VI. New species of large trees from Madagascar. *Candollea* 76: 201–236. In English, English and French abstracts. DOI: http://dx.doi.org/10.15553/c2021v762a3

An ongoing revision of the *Ebenaceae* of the Malagasy region has focused in particular on the species of large trees potentially vulnerable to illegal exploitation for their hardwood. Eighty two of the c. 255 species of *Diospyros* L. in Madagascar have been identified as large trees, among which 15 new species are described and illustrated (i.e. *Diospyros ambanjensis* G.E. Schatz & Lowry, *Diospyros amborelloides* G.E. Schatz & Lowry, *Diospyros andohahelensis* G.E. Schatz & Lowry, *Diospyros beberonnii* G.E. Schatz & Lowry, *Diospyros beberonnii* G.E. Schatz & Lowry, *Diospyros crassipedicellata* G.E. Schatz & Lowry, *Diospyros grandiflora* G.E. Schatz & Lowry, *Diospyros melanocarpa* G.E. Schatz & Lowry, *Diospyros melanocarpa* G.E. Schatz & Lowry, *Diospyros mimusops* G.E. Schatz & Lowry, *Diospyros quadrangularis* G.E. Schatz & Lowry, *Diospyros rakotovaoi* G.E. Schatz & Lowry, and *Diospyros taikintana* G.E. Schatz & Lowry). Risk of extinction assessments using the IUCN Red List criteria indicate that 12 species are threatened.

### Résumé

SCHATZ, G.E., P.P. LOWRY II, H.N. RAKOUTH & R. RANDRIANAIVO (2021). Études taxonomiques du genre Diospyros (Ebenaceae) de la région malgache. VI. Nouvelles espèces de grands arbres à Madagascar. *Candollea* 76: 201–236. En anglais, résumés anglais et français. DOI: http://dx.doi.org/10.15553/c2021v762a3

Une révision en cours des *Ebenaceae* de la région malgache s'est porté en particulier sur les espèces de grands arbres qui peuvent être exposées à une exploitation illégale pour leur bois de qualité. Quatre-vingt deux des c. 225 espèces de *Diospyros* L. à Madagascar sont considérées comme des grands arbres dont 15 espèces sont décrites et illustrées ici (i.e. *Diospyros ambanjensis* G.E. Schatz & Lowry, *Diospyros ambonelloides* G.E. Schatz & Lowry, *Diospyros andohahelensis* G.E. Schatz & Lowry, *Diospyros antsirananae* G.E. Schatz & Lowry, *Diospyros bardotiae* H.N. Rakouth, G.E. Schatz & Lowry, *Diospyros grandiflora* G.E. Schatz & Lowry, *Diospyros grandiflora* G.E. Schatz & Lowry, *Diospyros malandy* H.N. Rakouth, Randrianaivo, G.E. Schatz & Lowry, *Diospyros melanocarpa* G.E. Schatz & Lowry, *Diospyros minusops* G.E. Schatz & Lowry, *Diospyros quadrangularis* G.E. Schatz & Lowry, *Diospyros rakotovaoi* G.E. Schatz & Lowry et *Diospyros taikintana* G.E. Schatz & Lowry). Une évaluation préliminaire du risque d'extinction de chaque espèce selon les critères de la Liste Rouge de l'UICN indique que 12 espèces sont menacées.

# Keywords

EBENACEAE - Diospyros - Madagascar - Ebony - IUCN Red List - New species

Addresses of the authors:

GES: Missouri Botanical Garden, 4344 Shaw Blvd., St. Louis, Missouri 63110, U.S.A. E-mail: george.schatz@mobot.org

PPL: Missouri Botanical Garden, 4344 Shaw Blvd., St. Louis, Missouri 63110, U.S.A.; Institut de Systématique, Évolution, et Biodiversité (ISYEB), MNHN, CNRS, Sorbonne Université, École Pratique des Hautes Études, Université des Antilles, C.P. 39, 57 rue Cuvier, 75005 Paris, France.

HNR: Mention Biologie et Ecologie Végétales, Faculté des Sciences, Université d'Antananarivo, B.P. 906, Antananarivo 101, Madagascar.

RR: Missouri Botanical Garden, Madagascar Research and Conservation Program, B.P. 3391, Antananarivo 101, Madagascar.

Submitted on November 23, 2020. Accepted on June 7, 2021.

First published online on July 7, 2021.

 $ISSN: 0373-2967 - Online \ ISSN: 2235-3658 - \textit{Candollea} \ 76(2): 201-236 \ (2021)$ 

© CONSERVATOIRE ET JARDIN BOTANIQUES DE GENÈVE 2021

# Introduction

A comprehensive review of the family Ebenaceae on Madagascar was initiated a decade ago to revise and update the treatment published in the Flore de Madagascar et des Comores (Perrier de la Bâthie, 1952), which had proven to be incomplete and out of date after many decades of botanical inventory work had increased the available number of collections more than tenfold. As an initial step, Schatz & Lowry (2011) transferred 12 species from the previously recognized genera Maba J.R. Forst. & G. Forst. and Tetraclis Hiern into Diospyros L. In the same paper, several taxa recognized by Perrier De LA BÂTHIE (1952) were placed in synonymy, reducing the total number of accepted species from 97 in the Flore (along with 15 infraspecific taxa) to 84 species (and no infraspecific taxa). Careful examination of the more than 4000 collections now available has also revealed about 155 new species (MADAGASCAR CATALOGUE, 2021), including 31 that have already been described (Linan et al., 2021; Schatz & Lowry, 2018, 2020; Schatz et al., 2020) and 21 that will soon be published (Schatz et al., in press; Mas et al., unpubl. data), leaving some 100 additional new species to be described.

Diospyros is the source of ebony wood, a valuable and highly prized hardwood obtained from various species throughout most of the range of this primarily tropical genus. Madagascar has long been a source of high quality ebony, but a massive increase in illegal and unsustainable exploitation of precious woods prompted CITES (the Convention on International Trade in Endangered Species of Wild Fauna and Flora) to place Malagasy Diospyros on its Appendix II in 2013, resulting in a total embargo on international trade (Mason et al., 2016). Pressure has been mounting in Madagascar to end the embargo in order to generate badly needed foreign exchange, but sustainable exploitation would require careful control and regulation along the entire supply chain, from standing trees and cut logs to sawn wood and finished products ready for export, coupled with strict limits on the harvest of exploitable species and a total ban on those that require conservation. An effective regulatory system would also depend on accurate identification of trees, logs, and cut wood, which is currently impossible for Malagasy Diospyros since half of the species are not yet named and no reliable identification tools are available, including for material that lacks flowers and fruits. In order to address this need, a consortium of Malagasy and international institutions established in 2017 is conducting an ambitious project that involves (1) field work to develop a reference library comprising voucher herbarium specimens, wood, bark, leaves, and silica gel-dried wood and leaf material, which is being used both for (2) taxonomic work to delimit and describe all Diospyros species that are potential sources of precious woods and for (3) an integrated program to elucidate morphological characters, wood anatomical and spectrometric features, and DNA barcodes that can be used to (4) develop practical,

reliable field identification tools and forensic wood identification protocols.

Very little information is available on which species of Diospyros in Madagascar produce ebony wood of commercial value. Fifteen species have herbarium or literature records indicating that they are exploited [D. calophylla Hiern, D. clusiifolia (Hiern) G.E. Schatz & Lowry, D. ebenifera (H. Perrier) G.E. Schatz & Lowry, D. erythrosperma H. Perrier, D. ferrea (Willd.) Bakh., D. gracilipes Hiern, D. haplostylis Boivin ex Hiern, D. humbertiana H. Perrier, D. implexicalyx H. Perrier, D. manampetsae H. Perrier, D. mapingo H. Perrier, D. occlusa H. Perrier, D. perrieri Jum., D. sphaerosepala Baker, and D. toxicaria Hiern], and three additional species may be exploited [D. fuscovelutina Baker, D. hazomainty H. Perrier, and D. meeusiana (H. Perrier) G.E. Schatz & Lowry], but another 64 species are known to reach 20 m tall and/or 20 cm in diameter at breast height (DBH), suggesting that they may become large enough trees to be potential sources of exploitable hardwood. These include 31 described species and 18 new species currently being described in the other papers cited above. In the present contribution we describe the 15 remaining large tree species, thereby finalizing the process of naming all potentially exploitable *Diospyros* in Madagascar.

The description presented below for each new species is accompanied by an illustration and a risk of extinction assessment according to the IUCN Red List Categories and Criteria (IUCN, 2012), for which the area parameters of Extent of Occurrence (EOO) and Area of Occupancy (AOO) were calculated using GeoCAT (2021). Specimen records can be accessed for each species via the *Catalogue of the Plants of Madagascar* (Madagascar Catalogue, 2021). However, since each of the species described here can form large enough trees to be potentially exploited as a source of ebony, geocoordinates and detailed locality data have been withheld and public access to this information through the Madagascar Catalogue (2021) has been restricted.

# **Taxonomy**

Diospyros ambanjensis G.E. Schatz & Lowry, sp. nov. (Fig. 1).

Holotypus: MADAGASCAR. Reg. Diana [Prov. Antsiranana]: forêt de Bekalonoro, 19.IX.2013, fr., Rasoanaivo 93 (MO-6857393!; iso-: G [G00341884]!, P [P01047888]!, TAN!).

Diospyros ambanjensis G.E. Schatz & Lowry resembles other members of the Tetraclis group in having fauve to rusty indumentum, leaves generally with a mucronate apex, male flowers borne in cymose to pseudo-umbellate inflorescences, and often valvate corolla aestivation, but is distinguished by having spiral to pseudo-verticillate phyllotaxy, the shoot apex

bearing numerous cataphylls prior to extension, and large leaves  $(11-37 \times 2.4-5.5 \text{ cm})$ .

Tree 6-16 m tall, 12-30 cm DBH. Young stems terete, densely covered with erect, brown to fauve trichomes c. 0.2-0.3 mm long, the shoot apex densely covered with numerous (c. 80) cataphylls prior to extension. Leaves arranged spirally to pseudo-verticillate along stem; lamina 11-37 × 2.4-5.5 cm, narrowly oblanceolate, coriaceous, sparsely covered above with erect, golden to fauve trichomes c. 0.8-1.2 mm long, more densely along the midvein, or glabrous, sometimes drying somewhat glaucous, initially rather densely covered below with erect, golden to fauve trichomes, more densely along the midvein, glabrescent, base long attenuate and slightly decurrent along petiole, margin revolute and densely ciliate initially, glabrescent, apex acute to rounded with a distinct mucron to 6 mm long, midvein impressed to flat above, distinctly raised below, venation eucamptodromous to weakly brochidodromous, often indistinct, with 13-23 secondary veins per side, flat to slightly raised above and below, tertiary venation reticulate; petiole 8-15 mm long, 2-3 mm in diam., densely covered with erect, brown to fauve trichomes c. 0.5-1 mm long. Male flowers borne in axillary, cymose to pseudo-umbellate inflorescences, composed of 3–7 flowers, the main axis (peduncle) 15-40 mm long, 0.5-1 mm in diam., densely covered with erect, fauve trichomes c. 1.5–2 mm long, pedicel 3–6 mm long, 1-1.5 mm in diam., densely covered with fauve trichomes c. 0.5-0.8 mm long; calyx urceolate,  $4 \times 4$  mm, irregularly 4-lobed, the lobes  $1-2 \times 2-3$  mm, triangular, densely covered with semi-erect, fauve trichomes c. 0.2-0.3 mm long; corolla narrowly oblongoid-ellipsoid, 7-9 mm long, densely covered outside with appressed, fauve trichomes c. 0.8-1 mm long, 4-lobed, the lobes valvate,  $2-3 \times 2-3$  mm, triangular; stamens 26, subsessile, attached to the corolla at two levels, just above the middle and c. 1 mm higher, anthers 2-3 mm long, narrowly sagittate; pistillode narrowly ovoid, 5 mm long, 2 mm in diam., densely covered with stiff, semi-appressed, fauve trichomes c. 1 mm long, crowned by 2-3(-4?) stylodes. Female flowers axillary, solitary, sessile to subsessile, subtended by several ovate bracts  $4-6 \times 4-5$  mm, apex abruptly acuminate; calyx urceolate,  $8-9 \times 9-10$  mm, 4-lobed, the lobes broadly triangular to ovate,  $3-5 \times 5-7$  mm, apex abruptly acuminate, densely covered outside and inside with erect, chocolate brown trichomes c. 0.2-0.3 mm long; corolla ellipsoid, 13 mm long, 9-10 mm in diam., densely covered outside with appressed, chocolate brown trichomes c. 0.8-1 mm long, except at base, glabrous inside, 4-lobed, the lobes valvate,  $2-3 \times 3-4$  mm, triangular, staminodia absent; ovary spherical, 7 mm in diam., densely covered with semi-appressed, stiff, chocolate brown to fauve trichomes c. 0.5 mm long, styles 4,3 mm long, 0.6 mm in diam., fused for 1 mm at the base, densely covered with golden fauve trichomes c. 0.5-0.8 mm long at the base, progressively shorter toward the glabrous apex; stigma irregularly lobed and flattened, 1–2 mm across; ovules 8. *Fruits* solitary, axillary, sessile to subsessile; fruiting calyx accrescent, 14–16 mm  $\times$  c. 25 mm, the lobes 16–21  $\times$  13–19 mm, margins flat, densely covered with very short, erect, fauve trichomes c. 0.5–0.8 mm long; fruit spherical to slightly ellipsoid, 35–40 mm in diam., initially densely covered with appressed and erect, fauve trichomes c. 1–1.5 mm long, glabrescent except for the areas protected by the calyx. Seeds not seen.

Vernacular names. – "Hazojoby" (Rasoanaivo 93), "Mapingo" (Service Forestier 10640).

Distribution and ecology. – Diospyros ambanjensis is known from the Ampasindava and Ambato Peninsulas and from Ankitsika (Madagascar Catalogue, 2021), all of which are located in the Sambirano region of northwestern Madagascar. It occurs in low-elevation subhumid forest.

Phenology. – Material of *Diospyros ambanjensis* has been collected in flower in November and December, and fruits have been collected in September.

Conservation status. – Diospyros ambanjensis has a geographic range in the form of an Extent of Occurrence of 1703 km² and a minimum Area of Occupancy of 20 km². It is present in the Ampasindava protected area, but elsewhere it is threatened by forest clearing for agriculture, fire, grazing, and exploitation for firewood and house construction material, all of which will result in continuing decline. With respect to the most serious plausible threat of forest clearing for agriculture, D. ambanjensis exists at five locations, and was recently assessed for its risk of extinction as "Endangered" [EN B1ab(i,ii,iii,iv,v)+2ab(i,ii,iii,iv,v)] (IUCN, 2021).

Notes. – Diospyros ambanjensis is a member of the Tetraclis group, characterized by often fauve to rusty indumentum, leaves generally with a mucronate apex, male flowers borne in cymose inflorescences, and often valvate corolla aestivation. Other members of the group include D. clusiifolia, D. erythrosperma, D. fuscovelutina, D. parifolia H. Perrier, D. urschii H. Perrier, and D. vescoi Hiern, as well as five additional new species described below (viz. D. antsirananae G.E. Schatz & Lowry, D. beberonnii G.E. Schatz & Lowry, D. crassipedicellata G.E. Schatz & Lowry, D. mimusops G.E. Schatz & Lowry, and D. rakotovaoi G.E. Schatz & Lowry) and several others awaiting description. Within the Tetraclis group, D. ambanjensis can be distinguished by its spiral to pseudo-verticillate phyllotaxy, the shoot apex bearing numerous cataphylls prior to extension.

Additional specimens examined. – Madagascar. Reg. Diana [Prov. Antsiranana]: Ampasindava, forêt de Betsitsika, 4.XI.2009, ♂ fl., Gautier et al. 5309 (G, P); Ambato Forêt Classée, 22.XI.1996, ♀ fl., Randrianaivo

et al. 24 (MO, P, TAN); Ankitsika, Ambanja, 8.IX.1954,  $\lozenge$  fl., Service Forestier 10640 (P, TEF); Ampasindava, forêt de Bongomihiravavy, 13.XII.2008,  $\lozenge$  fl., Tabinarivony et al. 211 (G, P, TEF).

*Diospyros amborelloides* G.E. Schatz & Lowry, **sp. nov.** (Fig. 2A, 3).

Holotypus: MADAGASCAR. Reg. Atsinanana [Prov. Toamasina]: Betampona Strict Nature Reserve, 13.I.2017, Schatz et al. 4466 (MO-6443100!; iso-: BR!, CAS!, G [G00341895]!, K!, P!, TAN!, WAG!, W!).

Diospyros amborelloides G.E. Schatz & Lowry most closely resembles D. erinacea (H. Perrier) G.E. Schatz & Lowry in having elliptic leaves that are chartaceous to subcoriaceous and have an attenuate base, axillary cymose male inflorescence with ellipsoid male flower buds, 1-several ovoid fruits per leaf axil, and a cupular fruiting calyx with an entire margin, but differs by having leaves with an acute to acuminate apex (vs. rounded) and a larger and wider lamina (largest blade  $9.5-15.5 \times 4.5-7.2$  cm vs.  $6-7.5 \times 2-3.1$  cm), and larger fruit ( $11 \times 6.5-7$  mm vs.  $6-7 \times 5$  mm).

Tree 4-18 m tall, 12-40 cm DBH. Young stems terete, glabrous. Leaves distichous, lamina 8-15.5 × 3.6-7.2 cm, elliptic, membranous, glabrous above and below, base long attenuate, margin flat, apex acute to acuminate, acumen 5–15 mm long, midvein flat to very slightly raised above, raised below, narrowing from the base to the apex, venation brochidodromous, with 7–12 secondary veins per side, slightly raised above and below, tertiary venation reticulate, weakly raised above and below; petiole 3-10 mm long, 1 mm in diam., glabrous. Male flowers in axillary cymose inflorescences, with 5-8 inflorescences per node, each with 1-5 flowers, 9-21 mm long, the axes slender, 0.5 mm in diam., moderately covered with semi-erect, grayish trichomes 0.1-0.2 mm long; flowers subsessile; calyx urceolate,  $2.5-3 \times 2.5-3$  mm, unlobed, the margin entire, sparsely covered outside with appressed, grayish trichomes 0.1–0.2 mm long, glabrous inside; corolla in bud black, densely covered outside with appressed black trichomes 0.2 mm long, glabrous inside; stamens 10-20, inserted at the base of the corolla in a single whorl, filaments 0.2 mm long, anthers 1.5 mm long, lanceolate; pistillode absent. Female flowers not seen. Fruits axillary, 2-3 infrutescences per axil, each with 1-3 fruits, often with evidence of 4 total subsessile flowers per female inflorescence, the axes densely covered with semi-erect, grayish trichomes 0.1-0.2 mm; fruiting calyx cupuliform,  $3.5-5 \times 6-8$  mm, entire, sparsely covered with semi-erect, grayish trichomes 0.1-0.2 mm long, glabrescent; fruit ovoid, 11 × 6.5-7 mm, glabrous, apex acute, crowned by the style/stigma remnant 1 mm long. Seeds 4, ovoid, 6 × 2–3 mm, black, shiny.

Etymology. - The specific epithet refers to the fact that male individuals of *Diospyros amborelloides* in flower resemble

Amborella trichopoda Baill. (Amborellaceae), an emblematic species endemic to New Caledonia whose phylogenetic position is sister to all other flowering plants (PONCET et al., 2019).

Vernacular names and uses. – "Hazomafana" (Réserves Naturelles 9127, Service Forestier 6149, Service Forestier 21889). Furniture and house construction (Service Forestier 21889).

Distribution and ecology. – Diospyros amborelloides occurs primarily in northeastern Madagascar, from Betampona reserve north to the area around the Baie d'Antongil, with outlying subpopulations in the Galoko-Kalobinono and Montagne d'Ambre protected areas in the northwest (Madagascar Catalogue, 2021). It occurs in low- to midelevation humid forest.

*Phenology.* – Flowering material of this species has been collected in September, and fruits have been collected in March, July, September, November, and December.

Conservation status. – Diospyros amborelloides has a geographic range in the form of an Extent of Occurrence of 45,633 km² and a minimum Area of Occupancy of 36 km². It is present in four protected areas, Betampona, Masoala, Montagne d'Ambre, and Zahamena. Outside of the protected areas, it is threatened by forest clearing for agriculture, fire, grazing, and exploitation for firewood and house construction material, all of which will result in continuing decline. With respect to the most serious plausible threat of forest clearing for agriculture, D. amborelloides exists at nine locations, and was recently assessed for its risk of extinction as "Vulnerable" [VU B2ab(i,ii,iii,iiv,v)] (IUCN, 2021).

Notes. – Diospyros amborelloides most closely resembles another humid forest species occurring in eastern Madagascar, D. erinacea, with which it shares elliptic, chartaceous to subcoriaceous leaves with an attenuate base, axillary cymose male inflorescences, ellipsoid male flower buds, ovoid, acorn-like fruits borne singly or more often in groups of up to 4–5 per leaf axil, and a cupular fruiting calyx with an entire margin. Diospyros amborelloides can be distinguished from D. erinacea by having leaves with an acute to acuminate (vs. rounded) apex and an elliptic (vs. narrowly elliptic) lamina, the largest of which measures 9.5–15.5 × 4.5–7.2 cm (vs. 6–7.5 × 2–3.1 cm), and fruit that are 11 × 6.5–7 mm (vs. 6–7 × 5 mm).

Additional specimens examined. – MADAGASCAR. Reg. Analanjirofo [Prov. Toamasina]: Vavatenina, RNI de Zahamena, 9.VII.2003, y.fr., Andrianjafy et al. 395 (CNARP, MO, P, TEF); Maroantsetra, Anjahana, Hiaraka, 200 m, 3.IX.2002, & fl., Antilahimena 1329 (MO, P, TAN); Maroantsetra, Antsirabesahatany, Anjiahely, 23.XII.2002, y.fr., Antilahimena 1587 (MO, P, TAN); Anjorolava, Marosoraka, Maroantsetra, 27.IX.1952, & fl., Service Forestier 6149 (MO, P, TEF); Fénérive, Tanambao, Vatofasika, 25.IX.1964, & fl.,

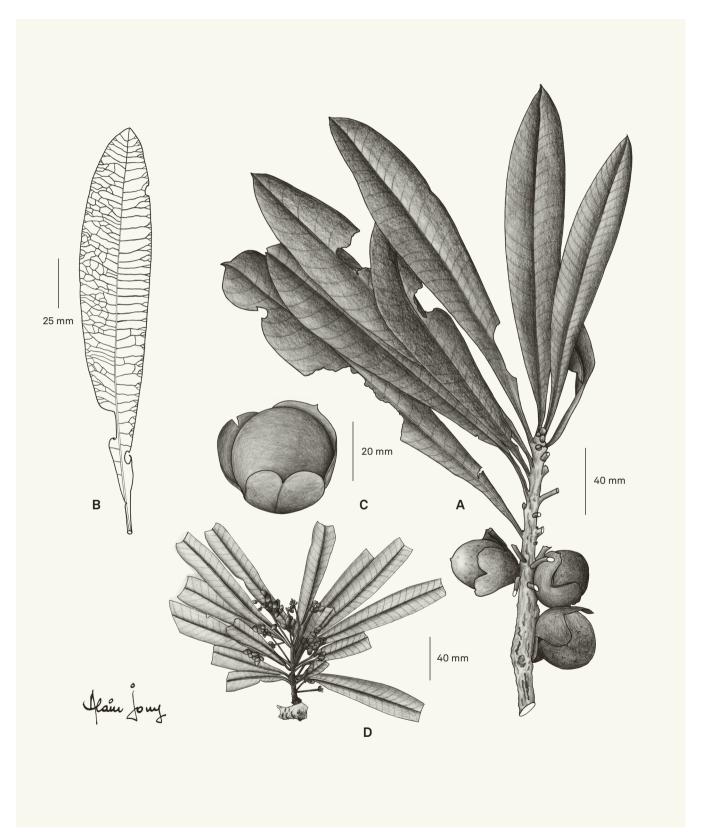


Fig. 1. – Diospyros ambanjensis G.E. Schatz & Lowry. A. Branch with fruits; B. Detail of leaf (abaxial surface); C. Fruit; D. Branch with male flowers. [A—C: Rasoanaivo 93, P; C: Tahinarivony et al. 211, P] [Drawing: Alain Jouy]

Service Forestier 21889 (G, MO, P, TEF); forêt de Sahavolamena, au S de Soanierana-Ivongo, 16–18.XI.1964, y.fr., Service Forestier 23799 (P, TEF); ibid. loco, 21.XII.1967, fr., Service Forestier 28123 (P, TEF). Reg. Atsinanana [Prov. Toamasina]: Vohimangitra, Ambodiriana [Betampona Reserve], 13.IX.1957, y.fr., Réserves Naturelles 9127 (MO, P, TAN). Reg. Diana [Prov. Antsiranana]: Ambilobe, Beramanja, Anketrabe, 2.XII.2007, fr., Rakotovao et al. 3882 (G, MO, P, TAN); Montagne d'Ambre, partie S, 4.III.2012, fr., Ramandimbimanana & Randimbiarison 413 (G, MO, P, TEF).

*Diospyros andohahelensis* G.E. Schatz & Lowry, **sp. nov.** (Fig. 4).

Holotypus: Madagascar. Reg. Anosy [Prov. Toliara]: Réserve N° 11 (Andohahela), 15.III.1987, fr., *Schatz & Nicoll 1244* (MO-3522351!; iso-: P [P03975070]!, TAN!, US [US03722051] image!, WAG [WAG.1180513] image!).

Diospyros andohahelensis G.E. Schatz & Lowry is distinguished from other members of the genus in Madagascar by the long (1–2 mm), erect indumentum on its young stems, and its ellipsoid, slightly asymmetrical fruits with a persistent stylar remnant, densely covered with appressed, light orange-brown trichomes 0.5–1.5 mm long.

Tree 4-7 m tall, 15-20 cm DBH. Young stems terete, glabrous or sparsely covered with straight, erect trichomes 1-2 mm long. Leaves distichous, lamina  $1.8-7 \times 0.7-2$  cm, narrowly ovate, membranous, glabrous on both surfaces, base obtuse to rounded, margin flat, apex acuminate, acumen 7–15 mm long, the very tip rounded, sometimes slightly falcate, midvein raised above, flat to slightly impressed below, venation weakly brochidodromous, obscure, secondary veins c. 8 per side, flat and indistinct above and below, tertiary venation reticulate; petiole 1-2 mm long, 1 mm in diam., canaliculate, glabrous. Male flowers 3-merous, solitary or paired in the axils of leaves, pedicel c. 1 mm long, < 1 mm in diam., with a pair of small rounded bracteoles 1 mm in diam. subtending the calyx, their margins ciliate; calyx narrowly cupuliform, 3 × 2.5 mm, the lobes broadly ovate-triangular, 2 × 2 mm, sparsely covered with short, appressed trichomes; corolla obconical, 6 mm long, lobes 4 × 3 mm, obovate, densely covered outside with short appressed trichomes, glabrous inside, slightly reflexed; stamens 9, attached at the base of the corolla, filaments 0.5 mm long, anthers 4 mm long, dehiscing by apical pores; pistillode absent. Female flowers not seen. Fruits axillary, solitary, pedicel in fruit 1.5 mm long, 1 mm in diam. at the base to 2.5 mm in diam. at the apex, rather densely covered with appressed light orangebrown trichomes 0.5-1.5 mm long; fruiting calyx broadly cupuliform,  $3.5-4 \times 6-7$  mm, very sparsely covered with short appressed trichomes c. 0.2 mm long, shallowly 3-lobed, the lobes 2 × 4 mm, broadly ovate, margin flat, pedicel scar 1.5 mm in diam.; fruit ellipsoid or less often narrowly obovoid or narrowly ovoid, slightly asymmetrical, 20–24 × 10–13 mm, apex apiculate from the persistent stylar remnant, apiculum 1.5-2 mm long, beige in vivo, black in sicco, densely covered

with appressed light orange-brown trichomes 0.5–1.5 mm long. *Seed* 1, narrowly ellipsoid to ovoid, 9 mm long, 3 mm in diam., greenish-brown with black verrucae.

Distribution and ecology. – Diospyros andohahelensis is known exclusively from the eastern portion of Parcel 1 of Andohahela National Park, at a single site just south of the Col de Maningotry on the road toward Ranomafana Sud, near the southern edge of the narrow forest corridor that connects the Anosy Mountains to the Tsitongambarika Protected Area in the Vohimena Mountains (MADAGASCAR CATALOGUE, 2021). It occurs in low-elevation humid forest.

*Phenology.* – Flowering material has been collected in November, and collections with fruit have been made in February and March.

Conservation status. – Diospyros andohahelensis has an extremely restricted geographic range in the form of an Extent of Occurrence of < 1 km² and an Area of Occupancy of < 1 km². Its distribution is wholly contained within the protected area of Andohahela. Nevertheless, it is present along the road that traverses Andohahela Parcel 1, and is thus threatened by ongoing exploitation of trees for firewood and house construction material, which will result in continuing decline of EOO, AOO, quality of habitat, number of locations/subpopulations, and mature individuals. With respect to the most serious plausible threat of exploitation of trees for firewood and house construction material, D. andohahelensis exists at 1 location, and was recently assessed for its risk of extinction as "Critically Endangered" [CR B1ab(i,ii,iii,iv,v)+2ab(i,ii,iii,iv,v)] (IUCN, 2021).

Notes. - Diospyros andohahelensis belongs to a loosely defined group of species in Madagascar characterized by 3-merous flowers and a small calyx that is generally cupuliform and entire or shallowly lobed, which includes several species previously placed by Perrier de la Bâthie (1952) in the genus Maba [e.g. D. erinacea, D. lokohensis (H. Perrier) G.E. Schatz & Lowry, D. myriophylla (H. Perrier) G.E. Schatz & Lowry, D. myrtifolia H. Perrier, D. olacinoides (H. Perrier) G.E. Schatz & Lowry, D. pervilleana (Baill.) G.E. Schatz & Lowry, D. quercina (Baill.) G.E. Schatz & Lowry, D. stenocarpa (H. Perrier) G.E. Schatz & Lowry, and D. tropophylla (H. Perrier) G.E. Schatz & Lowry, among others], as well as perhaps 25 additional new species that remain to be described. Within this group, D. andohahelensis can be distinguished by the long (1–2 mm), erect indumentum on its young stems, and its ellipsoid, slightly asymmetrical fruits with a persistent stylar remnant, densely covered with appressed, light orange-brown trichomes 0.5-1.5 mm long.

Additional specimens examined. – MADAGASCAR. Reg. Anosy [Prov. Toliara]: road to Andohahela, 13.XI.1989,  $\cite{Q}$  fl., McPherson 14467 (G, MO, P,



Fig. 2. – Photographs of *Diospyros* L. species. A. *Diospyros amborelloides* G.E. Schatz & Lowry, branch with immature fruit; B–D. *Diospyros antsirananae* G.E. Schatz & Lowry: B. Branch with fruit; C. Branch with fruit; D. fruit; E–F. *Diospyros bardotiae* H.N. Rakouth, G.E. Schatz & Lowry: E. Branch with immature fruit; F. Immature fruits. [A: *Rakotovao et al. 3882*; B: *Rakotonandrasana et al. 904*; C–D: *Rakotovarivelo 152*; E: *Randrianaivo 3273*; F: *Randrianaivo 3279*] [Photos: A: C. Rakotovao; B, E–F: R. Randrianaivo; C–D: N. Rakotovarivelo]

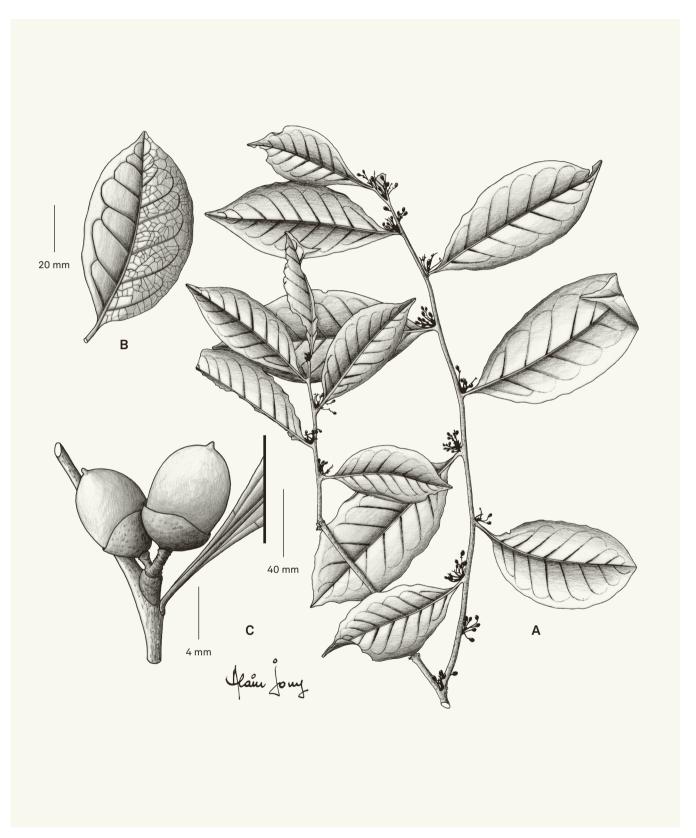


Fig. 3. – Diospyros amborelloides G.E. Schatz & Lowry. A. Branch with male inflorescences; B. Detail of leaf (adaxial surface); C. Fruits. [A, B: Antilahimena 1329, P; C: Rakotovao et al. 3882, P] [Drawing: Alain Jouy]

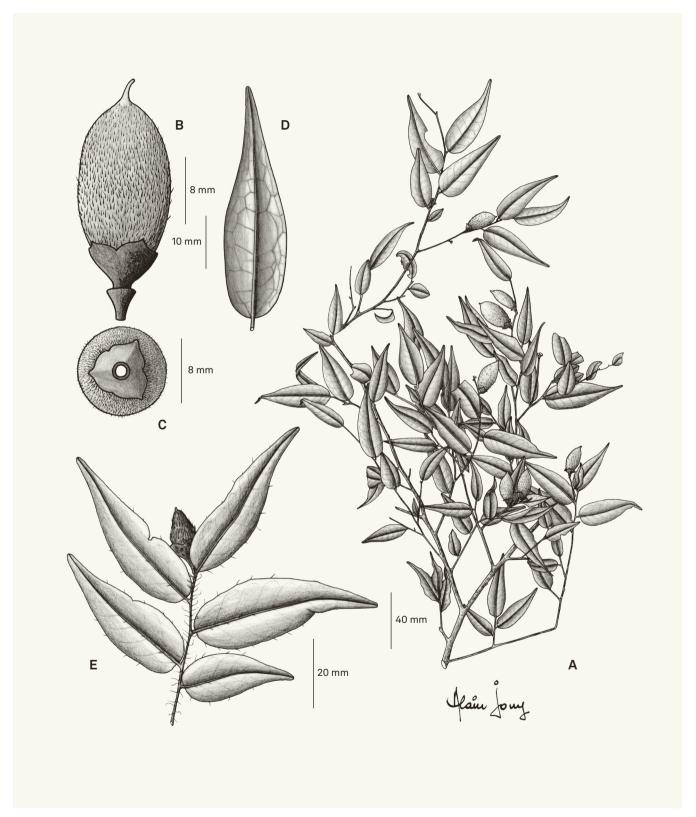


Fig. 4. – Diospyros andohahelensis G.E. Schatz & Lowry. A. Branch with fruits; B. Fruit; C. Fruiting calyx (seen from below); D. Detail of leaf (adaxial surface); E. Branch with leaves.

[A-D: Schatz & Nicoll 1244, P; E: Randriamampionona 203, P] [Drawing: Alain Jouy]

TAN, WAG); Andohahela, Parcelle 1, 16–24.III.1993, fr., Randriamampionona 203 (MO, P, TAN); ibid. loco, y.fr., 232 (MO, P, TAN); commune Isaka Ivondro, 11.II.2019, y.fr., Razakamalala et al. 8292 (TAN, MO, P); ibid. loco, 15.II.2019, y.fr, Razakamalala et al. 8297 (TAN, MO, P).

*Diospyros antsirananae* G.E. Schatz & Lowry, **sp. nov.** (Fig. 2B-D, 5).

Holotypus: MADAGASCAR. Reg. Diana [Prov. Antsiranana]: Massif de la Montagne des Français, 10.XI.1961, fr., Service Forestier 20378 (MO-6956004!; iso-: G [G00341736]!, P [P02091756, P02091757]!, TEF [TEF000890]!, W!).

Diospyros antsirananae G.E. Schatz & Lowry resembles other members of the Tetraclis group in having fauve to rusty indumentum, leaves generally with a mucronate apex, male flowers borne in cymose inflorescences, and often valvate corolla aestivation, but is distinguished by having dense, erect, curly, tangled rusty trichomes 1 mm long on the abaxial surface of its leaves and fruits densely covered with erect, rusty brown trichomes 2–3 mm long.

Tree 5-13 m tall, 10-20 cm DBH. Young stems terete to slightly flattened, densely covered with curly, erect, whitish to brown trichomes 0.2 mm long. Leaves distichous, lamina  $3.3-8.8 \times 2-4.2$  cm, elliptic to obovate, coriaceous, initially densely covered with minute, curly, erect whitish trichomes c. 0.2 mm long above, glabrescent, densely covered with erect, curly, tangled rusty trichomes 1 mm long below, base cuneate to rounded, margin revolute, apex acute to rounded, sometimes with a minute mucron on the leaves with acute apices, midvein impressed above, raised below, venation brochidodromous, with 7-14 secondary veins per side, slightly impressed to nearly obscure above, slightly raised below, tertiary venation reticulate; petiole 5–10 mm long, 1.5–2 mm in diam., canaliculate, densely covered with curly, erect, whitish to brown trichomes 0.2-0.8 mm long. Male flowers borne in axillary, pseudo-umbellate cymes, one inflorescence per axil, 3(-5) flowers per inflorescence, axes densely covered with erect, curly, rusty trichomes 0.2 mm long, primary axis (peduncle) 18–28 mm long, pedicel 4–7 mm long, 1.5 mm in diam.; calyx cupuliform, 4–4.5 × 6 mm, 4-lobed, the lobes broadly triangular,  $2 \times 4.5-5$  mm, densely covered outside with appressed, light brown trichomes 0.3-0.5 mm long, glabrous inside except for a ring of trichomes at the base; corolla cylindrical, 8 mm long, 5 mm in diam., 4-lobed, the lobes triangular, 2 × 2.5 mm, densely covered outside with appressed, light brown trichomes 0.3-0.5 mm long except glabrous along the margins of the lobes and at the base, glabrous inside; stamens c. 26, inserted on the corolla at two levels, ¼ and ½ from base, and of variable lengths, filaments 1.5 mm long, anthers 2 mm long, oblong, apex acute, dehiscing by apical pores; pistillode hemispherical, 2 mm long, densely covered with erect, golden trichomes

c. 1 mm long. Female flowers solitary, axillary, enclosed within several overlapping, distichous, circular bracts, 5 × 5 mm, densely covered with semi-erect, golden trichomes 0.1 mm long, pedicel 1-2 mm long, 2-2.5 mm in diam., densely covered with semi-erect, whitish to brown trichomes 0.2-0.5 mm long bearing a broadly ovate bract 2 × 3 mm, apex acute, densely covered with semi-erect, golden trichomes 0.1 mm long; calyx cupuliform, square in cross-section, 4 × 7 mm, 4-lobed, the lobes ovate-triangular, 7 × 7 mm, densely covered outside with semi-erect, light brown trichomes 0.3-0.5 mm long, glabrous inside except for a ring of trichomes at the base; corolla cylindrical, 7 mm long, 5 mm in diam., densely covered outside with appressed, light brown trichomes c. 0.3 mm long, glabrous inside except the lobes densely covered with appressed, light brown trichomes c. 0.3 mm long, 4-lobed, the lobes valvate, 3 × 4 mm, broadly ovate-triangular with a basal auricle on one side; ovary obloid, 4.5 mm long, 6 mm in diam., densely covered with erect, golden trichomes 1 mm long, styles 3 mm long, connate for 1.5 mm, with two free branches 1.5 mm long, stigma flat-topped, staminodia absent. Fruits axillary, solitary, pedicel in fruit 3 mm long, 3 mm in diam., densely covered with semi-erect, whitish to brown trichomes 0.2-0.5 mm long; fruiting calyx accrescent, broadly cupuliform, 12–15 × 25–28 mm, the lobes broadly triangular,  $10-12 \times 20-22$  mm, recurved, the margins often involute, densely covered with semi-erect, whitish to brown trichomes 0.2-0.5 mm long, with a prominent ridge extending from the base to sinus; fruit spherical to slightly obloid, 24-28 × 25-28 mm, the apex rounded or sometimes bluntly acute, densely covered with erect, rusty brown trichomes 2-3 mm long. Seeds 4, spherical wedge-shaped, 13 × 10 mm, black, matte.

Vernacular names and uses. - "Jobiampototra" (Randrianarivelo et al. 119), "Mapingo" (Rakotoarivelo 152).

House construction, artisanal woodworking (*Rakotoarivelo* 152).

Distribution and ecology. – Diospyros antsirananae is restricted to northern Madagascar, from Loky-Manambato protected area in the Daraina region to the extreme northern tip of the island at Cap d'Ambre, and including several sites around the city of Antsiranana (Madagascar Catalogue, 2021). It occurs in dry forest and occasionally in areas of transition toward more humid forest, on sand and calcareous substrate, including karstic formations ("tsingy").

*Phenology.* – Flowering material has been collected in February, April, and May; fruiting collections have been recorded throughout most of the year.

Conservation status. - Diospyros antsirananae has a geographic range in the form of an Extent of Occurrence of



Fig. 5. – Diospyros antsirananae G.E. Schatz & Lowry. A. Branch with fruits; B. Branch with female flowers; C. Branch with male inflorescences; D. Detail of leaf (abaxial surface); E. Schematic section of female flower; F. Schematic section of male flower; G. Fruit.
[A, D, G: Service Forestier 20378, P; B, E: Service Forestier 24707, P; C, F: Service Forestier 22700, P] [Drawing: Alain Jouy]

2783 km² and a minimum Area of Occupancy of 60 km². It is present in three protected areas, i.e., Andrafiamena Andavakoera, Loky-Manambato, and Montagne des Français. Outside of the protected areas, it is threatened by forest clearing for agriculture, fire, grazing, and exploitation for firewood and house construction material, all of which will result in continuing decline. With respect to the most serious plausible threat of forest clearing for agriculture, it exists at 13 locations. Therefore, *D. antsirananae* can be assessed for its risk of extinction as "Near Threatened" [NT], as it nearly qualifies as Vulnerable under criteria B1 and B2.

*Notes.* – *Diospyros antsirananae* is another member of the Tetraclis group (see notes under *D. ambanjensis* for a list of its diagnostic features), within which it can be distinguished by its abaxial leaf surface densely covered with erect, curly tangled rusty trichomes 1 mm long.

Additional specimens examined. - MADAGASCAR. Reg. Diana [Prov. Antsiranana]: Montagne des Français, 7.IV.2007, fr., Bardot-Vaucoulon 1655 (K, MO, P, TAN); Andrafiamena, 25.IX.2010, fr., Burivalova 44 (G, MO, P, TAN); Cap d'Ambre, XII.1966, Morat 1260 (TAN); Montagne des Français, 10. VIII. 2007, fr., Rakotoarivelo 152 (CNARP, MO, P, TAN); Mahavanona, Andranomanitra, 15.I.2005, fr., Rakotonandrasana et al. 904 (CNARP, MO, P, TAN); ibid. loco, 17.VI.2004, fr., Ramananjanahary et al. 26 (CNARP, MO, P, TAN); Montagne des Français, 24.I.2014, bud, Randrianaivo 2456 (BR, G, MO, P, TAN); ibid. loco, 11.IX.2004, fr., Randrianarivelo et al. 119 (MO, P, TAN); ibid. loco, 22.III.2007, y.fr., Ratovoson 1243 (CNARP, MO, P, TAN); Andavakoera, 5.XII.2007, fr., Ratovoson 1433 (CNARP, MO, P, TAN); forêt de Sahafary, bassin de la Saharaina, 25.IV.1963, & fl., Service Forestier 2700 (G, MO, P [3 sheets], TEF); forêt d'Analafondro, bassin inférieur du Rodo, 26.II.1964, A. fl., Service Forestier 23327 (G, MO, P [2 sheets], TEF, W); ibid. loco, 26.II.1964, bud, Service Forestier 23328 (G, MO, P, TEF); ibid. loco, 1.V.1966, ♂ fl., Service Forestier 24706 (P, TEF); ibid. loco et datum, ♀ fl., Service Forestier 24707 (BR, CAS, FHO, G, K, MO, NY, P [2 sheets], TEF, W, WAG, US). Reg. SAVA [Prov. Antsiranana]: Daraina, forêt de Bekaraoka Nord, 3.II.2019, ster., Karatra et al. 13 (DBEV, MO, P); ibid. loco, 19.II.2019, ster., Karatra et al. 63 (DEBV); Daraina, forêt d'Ampondrabe, 15.II.2019, ster., Karatra et al. 20 (DBEV, MO, P); SE of Ambilobe, near Daraina, on road to Vohemar (Iharana), 21.XII.1989, ster., McPherson 14745A (MO, TAN); Vohemar, commune rurale de Daraina, 1.II.2004, of fl., Ranirison et al. 378 (G, MO, P, TAN).

*Diospyros bardotiae* H.N. Rakouth, G.E. Schatz & Lowry, sp. nov. (Fig. 2E–F, 6).

Holotypus: MADAGASCAR. Reg. Diana [Prov. Antsiranana]: Ankarana, 17.X.1997, fr., *Bardot-Vaucoulon 801* (P [P00310033]!; iso-: K!, MO-5589264!, P [P00310034]!, TAN!).

Diospyros bardotiae H.N. Rakouth, G.E. Schatz & Lowry resembles other members of the Sclerophylla group in having male flowers borne in branched cymes and spherical fruit with accrescent, strongly reflexed calyx lobes, but is distinguished by having fruits with remarkably long pedicels (40–50 mm) and leaves in dried material that are usually dark in color, shiny above, and have evident, densely reticulate tertiary venation.

Tree 8-22 m tall, 7.5-21 cm DBH; bark black. Young stems terete, densely covered with semi-erect, whitish to light brown trichomes c. 0.1 mm long, glabrescent. Leaves distichous, borne 2–3 cm from one another, lamina  $5.6-11 \times 2.4-3.9$  cm, elliptic or sometimes narrowly elliptic, subcoriaceous, glabrous above, with moderately dense, semi-erect, whitish trichomes c. 0.3-0.5 mm long below, glabrescent, dark brownish-green to olive green both above and below, shiny and sometimes mottled grayish above, matte below, base cuneate to acute, symmetric to slightly asymmetric, margin slightly undulate, apex acute, the acumen 3–5 mm long, rounded, sometimes slightly retuse, midvein flat above, raised below, to 2 mm wide at the base, narrowing toward the apex, with semi-appressed, whitish to light brown trichomes c. 0.1 mm long, venation brochidodromous, with 10-14 secondary veins per side, raised above and below, tertiary venation reticulate, evident above and below; petiole 5-10 mm long, c. 1.5 mm in diam., shallowly canaliculate, darker than the lamina, densely covered with semiappressed, whitish to light brown trichomes c. 0.1 mm long, glabrescent. Male flowers in axillary cymes, with 2-4 orders of branching, composed of 24-44 flowers, the main axis (peduncle) 18-47 mm long, 1 mm in diam., densely covered with semi-erect, whitish or light brown to almost golden trichomes c. 0.1 mm long; pedicel 5-10 mm long, 1 mm in diam., densely covered with semi-appressed, whitish or light brown to almost golden trichomes c. 0.1 mm long; calyx cupuliform, c. 2 × 2 mm, shallowly 5-lobed, the lobes triangular,  $1-1.5 \times 1.5-2$  mm, densely covered with semi-erect, light brown to whitish trichomes c. 0.2 mm long, apex acute; corolla obovoid to oblanceoloid, 5-7 long, 1-1.5 mm in diam., white and scented in vivo, densely covered outside with appressed (silky), light brown to whitish trichomes c. 0.2-0.6 mm long, sparsely covered inside toward the margin with semi-erect, light brown to whitish trichomes c. 0.1–0.2 mm long; stamens 10, inserted toward the base of the corolla, filaments 1 mm long, anthers 1.5–2 mm long. Female flowers not seen. Fruits axillary, solitary, pedicel in fruit 40-50 mm long, 1-2 mm in diam., pendant, black, sparsely covered with erect, whitish trichomes 0.1–0.2 mm long, glabrescent, sometimes with minute bract scars toward the middle; fruiting calyx strongly accrescent, the base forming a short collar c. 1-2 mm long, the fused base broadly cupuliform, 8–12 mm in diam, with dense light brown trichomes c. 0.2-0.6 mm long, the lobes  $7-21 \times 5-10$  mm, elliptic, adaxially convex, grayish-green in sicco, strongly reflexed, with sparse, whitish, semi-appressed trichomes c. 0.2-0.6 mm long on both surfaces, glabrescent, matte, venation raised, margins weakly revolute, apex obtuse to rounded; fruit spherical to obloid or ovoid, 19-20 × 17-25 mm, initially green in vivo, dark brown at maturity, shiny, smooth, initially with whitish to light brown trichomes c. 0.3-0.8 mm long, glabrescent, apex apiculate. Seeds 6(-7), 1-2 per locule, spherical wedge-shaped,  $9-12 \times 5-7$  mm, dark brown to blackish, not shiny.

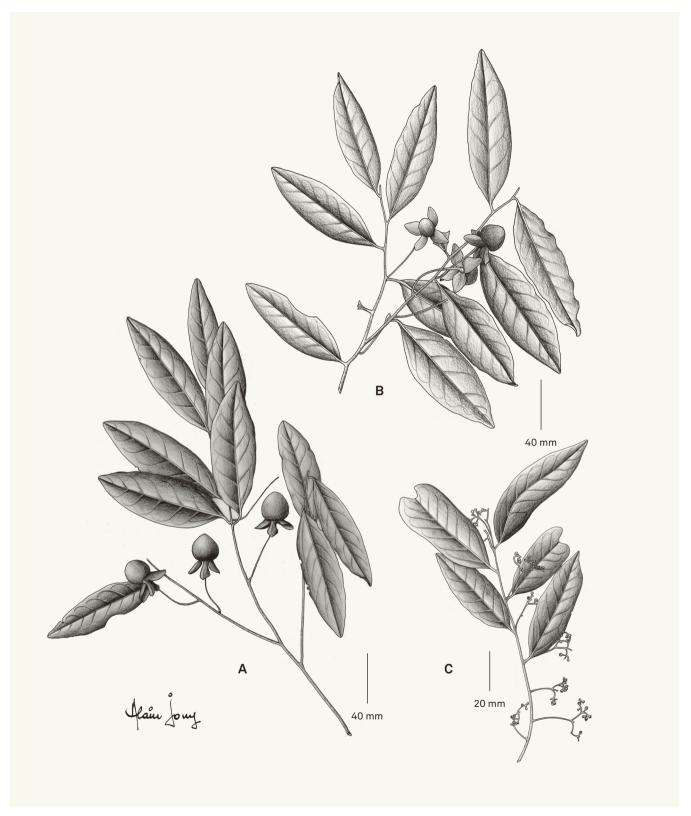


Fig. 6. – Diospyros bardotiae H.N. Rakouth, G.E. Schatz & Lowry. A. Branch with mature fruits; B. Branch with immature fruits; C. Branch with male inflorescences.

[A: Andrianantoanina 1019, P; B: Bardot-Vaucoulon 801, P; C: Service Forestier 10527, P] [Drawing: Alain Jouy]

Etymology. – This species is named in honor of Martine Bardot-Vaucoulon, who has passionately devoted most of her free time over the last 21 years to the exploration and documentation the flora of the Ankarana Special Reserve, where she has made more than 2000 collections, many representing new species, including *Diospyros bardotiae* and several other members of the genus that remain to be described.

Vernacular names. – "Mapingo" (Andrianantoanina 1019), "Doby-ampototra" (Bardot- Vaucoulon 1302).

Distribution and ecology. – Diospyros bardotiae is restricted to northern Madagascar, where it is known from two protected areas, Ankarana and Montagne d'Ambre. It occurs in dry semi-deciduous forest on basaltic laterite soil, to disturbed subhumid forest, swamps and wet land on ferrallitic-clay soil, from c. 100 to 365 m elevation.

Phenology. – Material of *Diospyros bardotiae* has been collected in flower in July and September, and fruiting collections have been recorded between December and February.

Conservation status. – Diospyros bardotiae has a geographic range in the form of an Extent of Occurrence of 556 km² and a minimum Area of Occupancy of 44 km². It is present in two protected areas, Ankarana and Montagne d'Ambre. Outside of the protected areas, it is threatened by forest clearing for agriculture, fire, grazing, and exploitation for firewood and house construction material, all of which will result in continuing decline. With respect to the most serious plausible threat of forest clearing for agriculture, *D. bardotiae* exists at 10 locations, and was recently assessed for its risk of extinction as "Vulnerable" [VU B1ab(i,ii,iii,iv,v)+2ab(i,ii,iii,iv,v)] (IUCN, 2021).

Notes. – Diospyros bardotiae is a member of the Sclerophylla group, characterized by male flowers borne in axillary, branched cymes and solitary, axillary, usually spherical fruit with the accrescent calyx lobes strongly reflexed 180 degrees. Other members of the group include D. bemarivensis H. Perrier, D. boinensis (H. Perrier) G.E. Schatz & Lowry, D. greveana H. Perrier, D. perglauca H. Perrier, D. perreticulata H. Perrier, D. sclerophylla H. Perrier, D. sakalavarum H. Perrier, and D. subbullata G.E. Schatz & Lowry, along with D. malandy H.N. Rakouth, Randrianaivo, G.E. Schatz & Lowry (described below) and as many as a dozen others awaiting description. Within the Sclerophylla group, D. bardotiae can be distinguished by its fruits with remarkably long pedicels and leaves in dried material that are usually dark colored, shiny above, and have evident, densely reticulate tertiary venation.

Additional specimens examined. – MADAGASCAR. Reg. Diana [Prov. Antsiranana]: Ankarana, 7.XII.2006, & fl., Andriamihajarivo 1042 (MO, P, TAN); Masorolava, Mahagaga, forêt d'Analabe, 23.IX.2007,

d fl., fr., Andriamihajarivo 1393 (MO, P, TAN); Ankarana, 11.VII.1994, Andrianantoanina 729 (MO, P, TAN); ibid. loco, 19.XI.1996, fr., Andrianantoanina 1019 (MO, P, TAN); ibid. loco, 19.II.1994, fr., Andrianarisata 36 (MO, P, TAN); ibid. loco, 24.I.2003, fr., Bardot-Vaucoulon 1302 (K, MO, P, TAN); ibid. loco, sine datum, fr., Debray 1190D (P); forêt de Maroatoalana, 7.I.2007, fr., Groeninckx 17 (BR, G, MO, P, TAN, WAG); Ankarana, 23.XI.1989, bud, fr., McPherson 14523 (MO, P, TAN); Montagne d'Ambre, 7.II.2012, fr., Ramandimbimanana 382 (G, P, TEF); Ankarana, 18.I.2014, Randrianaivo 2412 (BR, DBEV, G, MO, P, TEF); ibid. loco, 19.I.2014, Randrianaivo 2423 (BR, DBEV, G, MO, P, TEF); ibid. loco, 24.II.2016, fr., Randrianaivo 2872 (G. MO, P, TAN, TEF); ibid. loco, 9.XII.2018, fr., Randrianaivo 3271 (DBEV, G, MO, P, TAN); ibid. loco, fr., Randrianaivo 3272 (DBEV, G, MO, P, TAN); ibid. loco, fr., Randrianaivo 3273 (DBEV, G, MO, P, TAN); ibid. loco, fr., Randrianaivo 3274 (DBEV, G, MO, P, TAN); ibid. loco, 10.XII.2018, fr., Randrianaivo 3279 (DBEV, G, MO, P, TAN); ibid. loco, fr., Randrianaivo 3281 (DBEV, G, MO, P, TAN); ibid. loco, 21.III.2020, ster., Ravaoherinavalona 113 (DBEV, MO, P, TAN); ibid. loco, ster., Ravaoherinavalona 114 (DBEV, MO, P, TAN); ibid. loco, 24.III.2020, ster., Ravaoherinavalona 129 (DBEV, MO, P, TAN) ibid. loco, 26.III.2020, ster., Ravaoherinavalona 146 (DBEV, MO, P, TAN), ibid. loco, ster., Ravaoherinavalona 147 (DBEV, MO, P, TAN); ibid. loco, 13.VII.1954, & fl., Service Forestier 10527 (MO, P, TEF); ibid. loco, 1.IX.1954, Service Forestier 10659 (G, MO, P, TEF); ibid. loco, 16-28.I.1969, fr., Service Forestier 28708 (G, MO, P, TEF, W).

Diospyros beberonnii G.E. Schatz & Lowry, sp. nov. (Fig. 7).

Holotypus: Madagascar. Reg. Anosy [Prov. Toliara]: Parcelle 1 de la RN d'Andohahela, 10–27.IX.1993, fr., Randriamampionona 640 (MO-6956127!; iso-: BR!, CAS!, K!, F!, G [G00341740]!, MO-6956128!; NY!, OXF!, P [P03829510]!, PRE!, S!, TAN!, US!, W!, WAG!).

Diospyros beberonnii G.E. Schatz & Lowry resembles other members of the Tetraclis group in having fauve to rusty indumentum and leaves generally with a mucronate apex, but is distinguished by having white trichomes on its young stems and leaves, a small leaf lamina  $[(3-)4-8 \times 1-2.8 \text{ cm}]$ , a small fruiting calyx (5 mm long with lobes  $6-7 \times 7-8 \text{ mm}$ ), and small fruits (13–17 mm long).

Tree 14-20 m tall, 20-60 cm DBH. Young stems terete, densely covered with semi-appressed, whitish trichomes 0.5 mm long. Leaves distichous, lamina  $(3-)4-8 \times 1-2.8$  cm, narrowly ovate to elliptic to rarely obovate, chartaceous, initially sparsely covered with appressed, whitish trichomes c. 0.8 mm long above, more densely so along the midvein and margin, glabrescent, sparsely covered with appressed, whitish trichomes c. 0.5-0.8 mm long below, densely so along the midvein, base cuneate to attenuate, margin slightly thickened below, apex acute to acuminate, with a distinct mucron 1–1.5 mm long, midvein impressed above, prominently raised below, venation brochidodromous, with 10-12 secondary veins per side, tertiary venation reticulate, raised above and below, very evident above; petiole 4-8 mm long, 1 mm in diam., densely covered with semi-appressed, whitish trichomes 0.5 mm long, glabrescent. Male flowers not seen. Females flowers not seen. Fruits axillary, solitary, pedicel in fruit 5-7 mm long,

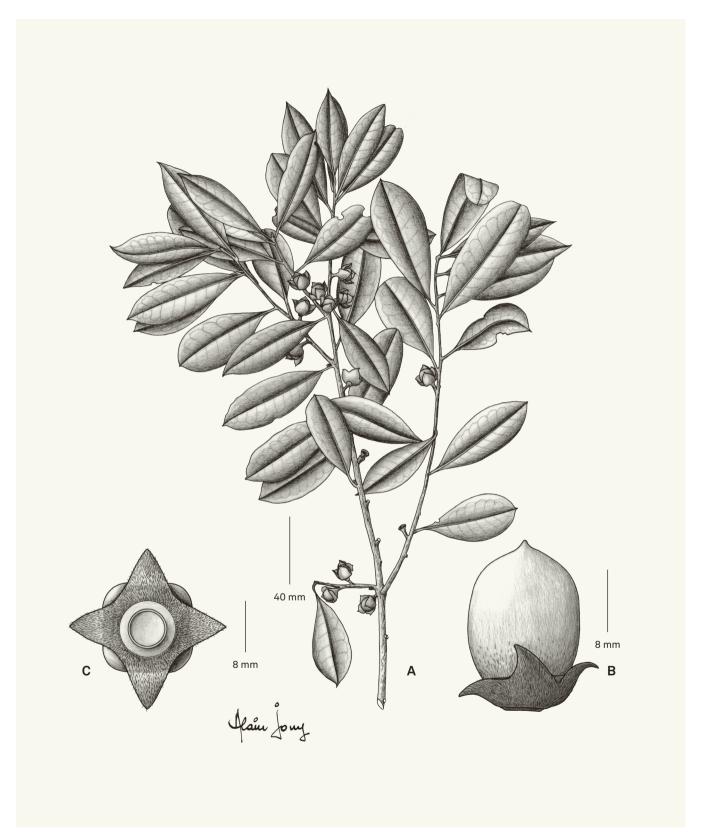


Fig. 7. – Diospyros beberonnii G.E. Schatz & Lowry. A. Branch with fruits; B. Fruit; C. Fruiting calyx (seen from below). [A: Randriamampionona 234, P; B—C: Randriamampionona 640, P] [Drawing: Alain Jouy]

4–5 mm in diam., very densely covered with erect, orangebrown trichomes 0.5–0.7 mm long completely obscuring the surface; fruiting calyx  $5 \times 12$ –13 mm, 4-lobed, the lobes ovatetriangular, 6– $7 \times 7$ –8 mm, very densely covered with erect, orange-brown trichomes 0.5–0.7 mm long, spreading, not appressed to the fruit wall, margin flat, pedicel scar 4 mm in diam.; fruit spherical to broadly ellipsoid, 13– $17 \times 15$ –17 mm, initially densely covered with appressed, orange-brown trichomes to 1.1 mm long, glabrescent except at the apex and at the base where protected by the calyx, crowned by a very short style/stigma remnant < 1 mm long, surface verrucose in sicco. *Seeds* 1–2?,  $11 \times 6$  mm, flattened ovoid, black, somewhat shiny.

Etymology. – This species honors Beberonn Randriamampionona, who began conducting botanical field work in 1989 and subsequently worked as a field botanist for Missouri Botanical Garden between 1992 and 1996, making nearly 1350 excellent collections, primarily in Andohahela National Park.

Distribution and ecology. – Diospyros beberonnii is known only from Parcel 1 of Andohahela National Park in southeastern Madagascar, with a single collection made just outside the southwestern limit of the parcel (Madagascar Catalogue, 2021). It occurs in low-elevation humid forest, occasionally in transition areas toward drier forest.

*Phenology.* – Fruiting material has been collected in March, July, and September.

Conservation status. – Diospyros beberonnii has a very restricted geographic range in the form of an Extent of Occurrence of 264 km² and an Area of Occupancy of 20 km². Its distribution is almost entirely contained within the protected area of Andohahela. Nevertheless, it is present near the road that traverses Andohahela Parcel 1 and at a site just outside the southwestern limit of the parcel, and is thus threatened by ongoing exploitation of trees for firewood and house construction material, which will result in continuing decline of quality of habitat and number of mature individuals. With respect to the most serious plausible threat of exploitation of trees for firewood and house construction material, D. beberonnii exists at five locations, and was recently assessed for its risk of extinction as "Endangered" [EN B1ab(iii,v)+2ab(iii,v)] (IUCN, 2021).

Notes. – Diospyros beberonnii is one of two species in the Tetraclis group (see notes under *D. ambanjensis* for a list of its diagnostic features) restricted to southeastern Madagascar, along with *D. mimusops* (described below). Within the group, it can be distinguished by the white trichomes on its young stems and leaves, and the overall small dimensions of its

lamina [ $(3-)4-8 \times 1-2.8$  cm], fruiting calyx (5 mm long with lobes  $6-7 \times 7-8$  mm), and fruit (13-17 mm long).

Additional specimens examined. – MADAGASCAR. Reg. Anosy [Prov. Toliara]: Andohahela, Parcelle 1, 16–24.III.1993, fr., Randriamampionona 234 (MO, P, TAN); ibid. loco, 8.VII.1994, fr., Randriamampionona 829 (MO, P, TAN); ibid. loco, 9.IX.2019, ster., Razakamalala & S. Andrianarivelo 8578 (DBEV, MO, P, TAN); ibid. loco, ster., Razakamalala & S. Andrianarivelo 8582 (DBEV, MO, P, TAN).

*Diospyros crassipedicellata* G.E. Schatz & Lowry, **sp. nov.** (Fig. 8, 9A–C).

Holotypus: Madagascar. Reg. Analanjirofo [Prov. Toamasina]: Farankaraina, 16.IX.1957, fr., Service Forestier 18318 (MO-6956005!; iso-: G [G00341737]!, P [P00722707, P03829422]!, TEF).

Diospyros crassipedicellata G.E. Schatz & Lowry resembles other members of the Tetraclis group in having fauve to rusty indumentum, leaves generally with a mucronate apex, male flowers borne in cymose inflorescences, and often valvate corolla aestivation, but is distinguished by having a distinctively thickened pedicel in fruit (5–9 mm in diam.) and narrow leaves (3.5–11.5 × 1.1–5 cm).

Tree 6-20 m tall, 11-30 cm DBH. Young stems terete, densely covered with straight, appressed or wavy semiappressed, whitish trichomes 0.5 mm long. Leaves distichous, lamina  $3.5-11.5 \times 1.1-5$  cm, elliptic to narrowly obovate to obovate, subcoriaceous to coriaceous, initially sparsely to densely covered with appressed trichomes 0.5 mm long above, more densely so along the midvein and margin, glabrescent, sparsely to densely covered with appressed trichomes to 0.8 mm long below, densely so along the midvein, base cuneate to attenuate, margin slightly thickened below, apex obtuse to acute to acuminate, occasionally rounded, usually with a distinct mucron 1–1.5 mm long, midvein slightly impressed above, prominently raised below, venation brochidodromous, with 9-12 secondary veins per side, tertiary venation reticulate, flat above and below; petiole 3–8 mm long, 1 mm in diam., densely covered with semi-appressed, whitish trichomes 0.5 mm long, glabrescent. Male flowers in cymose, axillary inflorescences, 1-3 inflorescences per axil, 2-7 flowers per inflorescence, or occasionally flowers solitary; inflorescence 5-17 mm long, the axes densely covered with erect, fauve trichomes c. 0.8-1 mm long, pedicel 3-9 mm long, 0.8-2 mm in diam., densely covered with erect, fauve trichomes c. 0.8–1 mm long; calyx cupuliform,  $3.5-4 \times 6-7$  mm, 4-lobed, the lobes triangular,  $2-4 \times 3-4$  mm, densely covered outside with erect, fauve trichomes c. 0.8-1 mm long, glabrous inside; corolla cupuliform, 8 mm long, 5 mm in diam., 4-lobed, the lobes valvate, 4 × 4 mm, ovate-triangular, rather densely covered outside with appressed trichomes to 0.5–0.8 mm long, rather densely covered inside with appressed trichomes c. 0.8-1 mm long

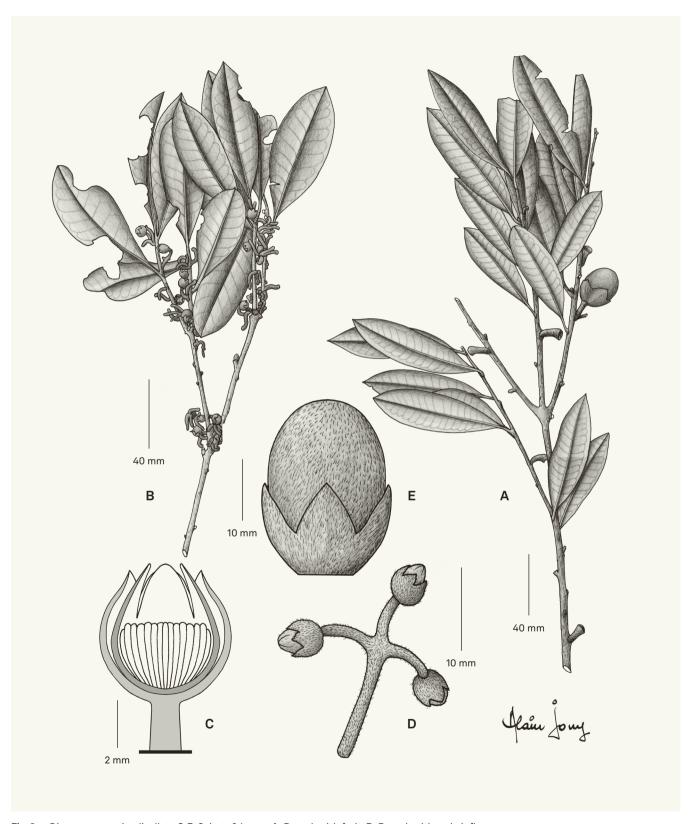


Fig. 8. – Diospyros crassipedicellata G.E. Schatz & Lowry. A. Branch with fruit; B. Branch with male inflorescences; C. Schematic section of male flower; D. Male inflorescence; E. Fruit.

[A, E: Service Forestier 18318, P; B-C: Service Forestier 12941, P] [Drawing: Alain Jouy]

from the point of insertion of the stamens to the apex, glabrous below the point of insertion of stamens, stamens 20, inserted on the corolla 1/3 from base, filaments 0.1 mm long, bearing a tuft of curved trichomes 1 mm long, anthers 1.8 mm long, apex apiculate, dehiscing by apical pores; pistillode absent, torus densely covered with erect trichomes. Females flowers not seen. Fruits axillary, solitary, pedicel in fruit 8-13 mm long, 5-9 mm in diam., very densely covered with erect, orangebrown trichomes 0.5-0.7 mm long completely obscuring the surface; fruiting calyx broadly cupuliform, 8–12 × 20 mm, 3-4-lobed, the lobes triangular to ovate to broadly ovate, 7–13 × 12–15 mm, densely covered with semi-erect, wavy, light brown trichomes c. 0.4-0.8 mm long, obscuring the calyx surface, erect and adhering to the fruit, margin flat, pedicel scar 5-6 mm in diam.; fruit ellipsoid, 25-38 × 20-25 mm, densely covered with semi-erect, wavy, light brown trichomes c. 0.4–0.8 mm long, obscuring the surface of the fruit. Seeds 4, 13 × 5 mm, flattened ovoid, black, shiny.

*Etymology.* – The specific epithet refers to the distinctively thickened pedicel in fruit.

Vernacular name. - "Hazomainty" (Service Forestier 10738).

Distribution and ecology. – Diospyros crassipedicellata occurs in eastern Madagascar, from Manombo reserve north to the area around the Baie d'Antongil, mostly in low-elevation humid forest near the coast, but also farther inland in midelevation humid forest at Ambalabe and Ankerana, both of which are situated within the Corridor Ankeniheny-Zahamena protected area (Madagascar Catalogue, 2021).

Phenology. – Flowering collections have been made from January to March, and fruiting material has been collected in May, June, and from August to November.

Conservation status. – Diospyros crassipedicellata has a geographic range in the form of an Extent of Occurrence of 32,769 km² and a minimum Area of Occupancy of 36 km². It is present in four protected areas, i.e., Analalava, Corridor Ankeniheny-Zahamena (Ambalabe and Ankerana), Masoala, and Manombo. Outside of the protected areas, it is threatened by forest clearing for agriculture, fire, grazing, and exploitation for firewood and house construction material, all of which will result in continuing decline. With respect to the most serious plausible threat of forest clearing for agriculture, D. crassipedicellata exists at seven locations, and was recently assessed for its risk of extinction as "Vulnerable" [VU B2ab(i,ii,iii,iv,v)] (IUCN, 2021).

Notes. - Diospyros crassipedicellata belongs to the Tetraclis group (see notes under D. ambanjensis for a list of its

diagnostic features), within which it can be distinguished by its distinctively thickened pedicel in fruit, which is 5–9 mm in diameter.

Additional specimens examined. - MADAGASCAR. Reg. Analanjirofo [Prov. Toamasina]: Ambanizana, 20.IX.2002, fr., Antilahimena 1421 (MO, P, TAN); ibid. loco, 9.XI.1994, fr., Rabe 195 (MO, P, TAN); ibid. loco, 27.VI.1994, fr., Randriamarosoa et al. 172 (MO, P, TAN); Farankaraina, 27.VIII.1954, fr., Service Forestier 10738 (MO, P, TEF); ibid. loco, 16.IX.1957, fr., Service Forestier 18318 (G, MO, P, TEF); Île Sainte-Marie, 18.V.1969, fr., Service Forestier 28842 (MO, P, TEF). Reg. Atsinanana [Prov. Toamasina]: Mahavelona, Foulpointe, 7.X.2011, fr., Andriamiarinoro & Amosa 247 (MO, P, TAN); Maroseranana, 24.III.2011, & fl., Antilahimena 7783 (MO, P, TAN); Analalava Reserve, 13 Sep 2017, fr., Grevais 120 (MO, P, TAN); ibid. loco, 15.I.2017, bud, Lowry et al. 7520 (MO, P, TAN); ibid. loco, 18.VI.2012, y.fr., Miandrimanana et al. 556 (MO, P, TAN); Ambalabe, Sahanionaka, 7.II.2011, A. Randrianasolo et al. 1385 (MO, P, TAN); Ankerana, 900 m, 14.III.2011, fl., Ravelonarivo & Edmond 3666 (MO, P, TAN). Reg. Atsimo-Atsinanana [Prov. Fianarantsoa]: Manombo, 27.VII.1955, ster., Réserves Naturelles 13956 (P); ibid. loco, 10.I.1955, & fl., Service Forestier 12940 (G, MO, P, TEF).

*Diospyros grandiflora* G.E. Schatz & Lowry, **sp. nov.** (Fig. 9D-F, 10).

Holotypus: MADAGASCAR. Reg. Atsinanana [Prov. Toamasina]: Betampona Reserve, 11.I.2017, fr., *Lowry et al.* 7482 (MO-6956129!; iso-: G [G00341741]!, K!, P [P00722717]!, TAN!, W!).

Diospyros grandiflora G.E. Schatz & Lowry most closely resembles D. toxicaria Hiern in its glabrous, coriaceous leaves with reticulate tertiary venation raised both above and below, but differs by its smaller leaf blades (6–12.5 × 3–5.4 cm vs.  $8-19 \times 4-6.5$  cm), often shorter petioles (10–13 mm vs. 6-18 mm), and larger female flowers with a calyx  $10-15 \times 16-18$  mm (vs.  $7-9 \times 4-5$  mm) and corolla c. 15 mm long (vs. 4-5 mm).

Tree 20-24 m tall, 20 cm DBH. Young stems terete, sparsely covered with appressed white to light brown trichomes 0.5 mm long. Leaves distichous, lamina 6-12.5 × 3-5.4 cm, elliptic to oblong to slightly ovate, coriaceous, glabrous above and below, shiny above, base obtuse to rounded, margin flat, apex rounded to acute, recurved, midvein impressed above, prominently raised below, venation weakly brochidodromous, with 6-10 secondary veins per side, slightly raised above and below, tertiary venation reticulate, slightly raised above and below; petiole 10-13 mm long, 1.5-2 mm in diam., canaliculate, glabrous. Male flowers solitary, axillary, sessile, surrounded by c. 4 distichous, concave bracts, broadly ovate to circular to oblate,  $2-7 \times 5-10$  mm, increasing in size from the basal bract to the apical bract, the apex deeply retuse, densely covered outside with appressed, fauve trichomes c. 0.3 mm long, glabrous inside; calyx in bud densely covered outside with appressed, fauve trichomes c. 0.5 mm long, glabrous inside; corolla

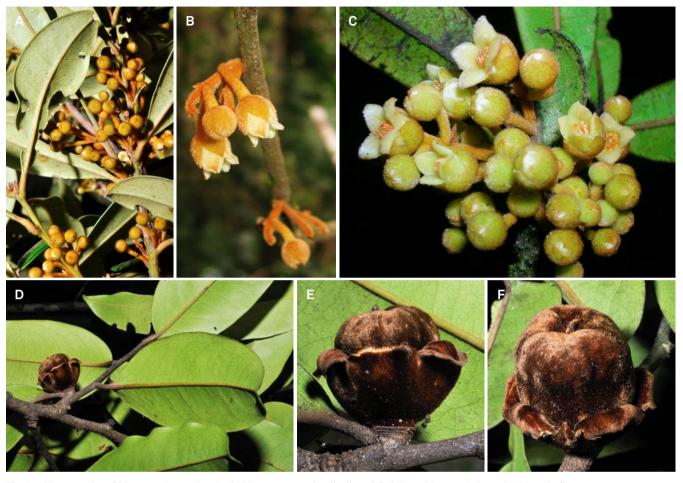


Fig. 9. – Photographs of *Diospyros* L. species. A—C. *Diospyros crassipedicellata* G.E. Schatz & Lowry: A. Branch with male flowers; B. Male inflorescence; C. Male flowers; D—F. *Diospyros grandiflora* G.E. Schatz & Lowry: D. Branch with fruit; E. Fruit (side view); F. Fruit (top view). [A: Lowry et al. 7520; B: Antilahimena 7783; C: Randrianasolo et al. 1385; D—F: Lowry et al. 7482] [Photos: A, D—F: P. Lowry; B: P. Antilahimena; C: F. Rakotoarivony]

in bud 4-5-lobed, densely covered outside with appressed, fauve trichomes c. 1 mm long from the lobes downward nearly to the base, glabrous elsewhere outside, glabrous inside; stamens 20, inserted on the torus, filaments 1 mm long, anthers 2 mm long, lanceolate, the apex acuminate; pistillode present, densely covered with short, erect trichomes. Female flowers solitary, axillary, surrounded by c. 8 oblate bracts, 13-15 × 17-21 mm, the apex deeply retuse, densely covered outside with appressed, fauve trichomes c. 0.5 mm long, glabrous inside, pedicel 2.5–3 mm long, 5 mm in diam.; calyx cupuliform to urceolate, 10-15 × 16-18 mm, 4-lobed, the lobes ovate-triangular, 6-7 × 8-10 mm, densely covered outside with erect, rusty brown trichomes 1 mm long; corolla c. 15 mm long, densely covered outside with appressed, rusty brown trichomes 3 mm long on the back of the lobes downward, mauve in vivo. Fruits axillary, solitary, pedicel in fruit 4-5 mm long, c. 8 mm in diam., with persistent, short, erect, dark ferruginous brown trichomes, with evident bract scars; fruiting calyx broadly hemispherical, c. 15 × 30 mm, 5-lobed, the lobes broadly triangular, c.  $8 \times 10$  mm, apex reflexed, densely covered with persistent, erect, dark ferruginous brown trichomes c. 1 mm long on both surfaces; fruit sub-spherical, slightly square in transverse section, c.  $25-30 \times 25-28$  mm, densely covered with persistent, erect, dark ferruginous brown trichomes, the apex depressed, with a persistent stylar remnant c. 3 mm long.

*Etymology.* – The specific epithet refers to the large size of the flowers.

Vernacular names. – "Hazomafana" (Réserves Naturelles 2642), "Hazomainty" (Réserves Naturelles 9731).

Distribution and ecology. – Diospyros grandiflora occurs in the Betampona reserve and a small remnant forest patch c. 11 km to the west-southwest (MADAGASCAR CATALOGUE, 2021), where it grows in mid-elevation humid forest.

*Phenology.* – Flowering material has been collected in July and August, and fruits are known from January.

Conservation status. – Diospyros grandiflora has an extremely restricted geographic range in the form of an Extent of Occurrence of < 5 km² and an Area of Occupancy of < 5 km². It is present in the protected area of Betampona. Outside of the protected area, it is threatened by forest clearing for agriculture and exploitation of trees for firewood and house construction material, which will result in continuing decline. With respect to the most serious plausible threat of forest clearing for agriculture, *D. grandiflora* exists at two locations, and was recently assessed for its risk of extinction as "Endangered" [EN B1ab(i,ii,iii,iv,v)+2ab(i,ii,iii,iv,v)] (IUCN, 2021).

Notes. – Diospyros grandiflora resembles D. toxicaria, a widespread species occurring in low- to mid-elevation humid forest in eastern Madagascar (Madagascar Catalogue, 2021), but has smaller leaves, with the lamina  $6-12.5\times3-5.4$  cm (vs.  $8-19\times4-6.5$  cm in D. toxicaria) and petioles 10-13 mm long (vs. 6-18 mm long), as well as considerably larger female flowers whose calyx is  $10-15\times16-18$  mm (vs.  $7-9\times4-5$  mm) and corolla c. 15 mm long (vs. 4-5 mm long). The female flowers of D. grandiflora are the largest of any known member of the genus on Madagascar.

Additional specimens examined. – MADAGASCAR. Reg. Atsinanana [Prov. Toamasina]: RN 1 [= Betampona], 9.VIII.1950, ♂ fl., Réserves Naturelles 2642 (TAN, P); ibid. loco, 10.VII.1958, ♀ fl., Réserves Naturelles 9731 (P, TEF); ibid. loco, 8.VII.1958, ♀ fl., Lewis 621 (MO, P); Betampona, 11.I.2017, ster., Lowry et al. 7481A (TAN, MO); Sahambala, 24.VII.2017, bud, G. Rakotonirina et al. 195 (K, MO, P, TAN).

Diospyros lowryi G.E. Schatz, sp. nov. (Fig. 11).

Holotypus: Madagascar. Reg. Analanjirofo [Prov. Toamasina]: Masoala Peninsula, 21.II.1989, fr., *Schatz & Lowry 2617* (MO-3706473!; iso-: K, P [P03975074]!, TAN [TAN001945]!, WAG [WAG.1180486] image!).

Diospyros lowryi G.E. Schatz is distinguished from other members of the genus in Madagascar by its ovate to elliptic, glabrous lamina with an abruptly short acuminate apex and its paired axillary infrutescences, each with 3–6 fruits, the ovoid to elliptic fruit densely covered with short, appressed, beige trichomes 0.2–0.4 mm long, rendering the fruit beige in vivo, light brown in sicco.

Tree 20–25 m tall, 25 cm DBH. Young stems terete, sparsely covered with minute, erect, white trichomes 0.1 mm long. Leaves distichous, lamina  $2.7-6 \times 1.2-3.3$  cm, ovate to elliptic, chartaceous, glabrous on both surfaces, base rounded to cuneate to acuminate, margin flat to slightly revolute, apex abruptly short acuminate, acumen 3-8 mm long, the very tip rounded, midvein very slightly impressed above, raised

below, venation brochidodromous, with 5-7 secondary veins per side, indistinct above, slightly raised below, tertiary venation reticulate; petiole 3-5 mm long, 1 mm in diam., rather sparsely covered with short, appressed trichomes c. 0.3 mm long, glabrescent. Male flowers in axillary cymose inflorescences of 2-4 flowers, 2-4 mm long, each flower subtended by a bracteole, the axes and bracteole orange-brown, pedicel c. 1 mm long, < 1 mm in diam., densely covered with short, appressed, light beige trichomes c. 0.3 mm long; calyx broadly urceolate, 1 × 1.5 mm, entire, rather densely covered with short, appressed, light beige trichomes c. 0.2-0.3 mm long; corolla obconical in bud; stamens c. 18, immature. Female flowers not seen. Fruits axillary, borne in paired cymose infructescences, each with 3-6 fruits, the axes densely covered with short, appressed, light brown trichomes c. 0.2-0.3 mm long; pedicel in fruit c. 1 mm long, c. 1.5-2 mm in diam., densely covered with appressed, light brown trichomes c. 0.2 mm long; fruiting calyx broadly cupuliform, 2 × 5–6 mm, entire, sparsely covered with appressed, light brown trichomes c. 0.2 mm long, margin entire, flat, dark chocolate brown in sicco, pedicel scar 1.5 mm in diam.; fruits ovoid to ellipsoid, 12-15 × 6-8 mm, slightly asymmetrical, beige in vivo, light brown in sicco, densely covered with short, appressed, beige trichomes c. 0.2-0.4 mm long, apex acute, shortly apiculate, apiculum 0.5 mm long. Seeds 1–3, ovoid to ellipsoid, 10–12 × 4–5 mm, glabrous, black, shiny.

Etymology. – The specific epithet honors my colleague Porter P. Lowry II, who has led the Missouri Botanical Garden's program in Madagascar since 1986. Although he is a specialist in *Araliaceae*, in 2009 he agreed to work together with me on a revision of Malagasy *Ebenaceae*, a collaboration that has surpassed our wildest expectations.

Vernacular names. – "Maintipototra" (Service Forestier 12978); "Maintimpototra à petites feuilles" (Service Forestier 15365).

Distribution and ecology. – Diospyros lowryi is restricted to the area around the Baie d'Antongil, where it has been collected at just two sites, near Ambanizana, situated just outside Masoala National Park, and at the Farankaraina Forestry Station, to the east of Maroantsetra (Madagascar Catalogue, 2021). It occurs in low-elevation humid forest.

*Phenology.* – Flowering material has been collected in November, and fruits in February and March.

Conservation status. – Diospyros lowryi has an extremely restricted geographic range in the form of an Area of Occupancy of 8 km². It is known from just outside the protected area of Masoala, where it is threatened by exploitation of trees for firewood and house construction material, which will result in continuing decline. With respect to the most serious

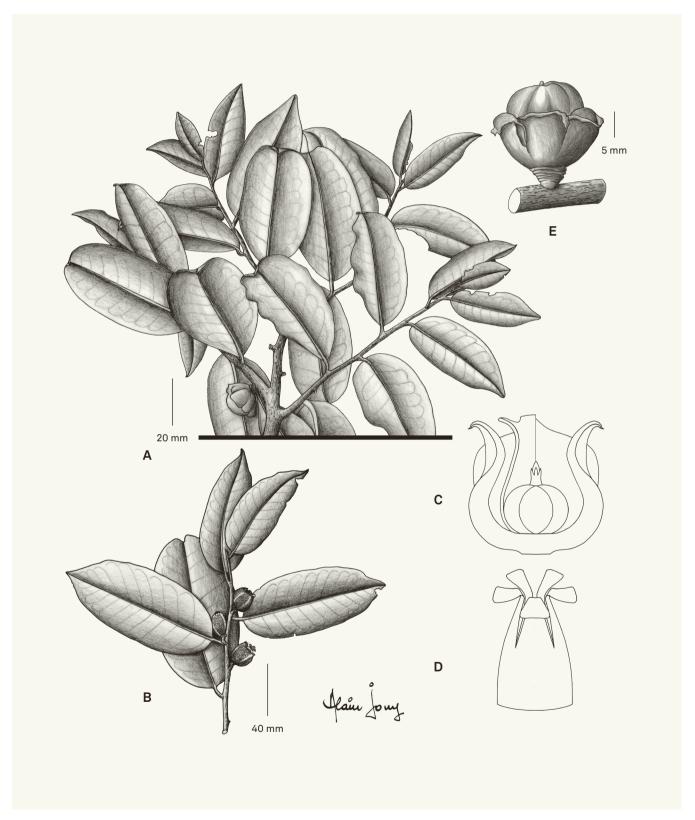


Fig. 10. – Diospyros grandiflora G.E. Schatz & Lowry. A. Branch in fruit; B. Branch with female flowers; C. Schematic section of female flower; D. Corolla of female flower; E. Fruit.

[A-D: Réserves Naturelles 9731, P; E: Lowry et al. 7482, from photo] [Drawing: Alain Jouy]

plausible threat of exploitation of trees for firewood and house construction material, *D. lowryi* exists at two locations, and it was recently assessed for its risk of extinction as "Endangered" [EN B2ab(iii,v)] (IUCN, 2021).

Notes. — Diospyros lowryi belongs to a loosely defined group of species in Madagascar characterized by 3-merous flowers and a small calyx that is generally cupuliform and entire or shallowly lobed, which includes several species previously placed by Perrier de la Bâthie (1952) in the genus Maba (see above under D. andohahelensis), as well as perhaps 25 additional new species that remain to be described. Within this group, D. lowryi can be distinguished by its ovate to elliptic, glabrous lamina with an abruptly acuminate apex and its axillary, paired infructescences, each with 3–6 fruits, the ovoid to elliptic fruits densely covered with appressed, beige trichomes 0.2–0.4 mm long, rendering the fruit beige in vivo, light brown in sicco.

Additional specimen examined. – MADAGASCAR. Reg. Analanjirofo [Prov. Toamasina]: Farankaraina, 4.III.1955, fr., Service Forestier 12978 (MO, P, TEF); ibid. loco, 25.XI.1955, & fl., Service Forestier 15365 (G, MO, P, TEF).

*Diospyros malandy* H.N. Rakouth, Randrianaivo, G.E. Schatz & Lowry, **sp. nov.** (Fig. 12, 13A).

Holotypus: MADAGASCAR. Reg. DIANA [Prov. Antsiranana]: Ankarana, 6.X.2018, fr., *Randrianaivo et al. 3240* (MO-6956007!; iso-: DBEV!, P [P00722673]!, TAN!).

Diospyros malandy H.N. Rakouth, Randrianaivo, G.E. Schatz & Lowry resembles other members of the Sclerophylla group in having spherical fruit with accrescent, strongly reflexed calyx lobes, but is distinguished by its leaves with a cuneate to rounded base, margin that is slightly revolute and undulate, and rounded to retuse apex, and densely reticulate, evident tertiary venation.

Shrub to tree, 2-25 m tall, 3-29.5 cm DBH. Young stems densely covered with short, erect, yellowish to pale brown trichomes 0.1 mm long. Leaves distichous, alternate, borne 15-25 mm from one another, lamina  $3.0-8.5 \times 2-5$  cm, obovate, chartaceous to subcoriaceous, discolorous in sicco, light grayish to pale olive green above, nearly glaucous below, matte on both surfaces, initially densely covered above with curly, semi-appressed, yellowish to pale brown trichomes c. 0.1 mm long, glabrescent, base cuneate to rounded, symmetric, margin slightly revolute and undulate, apex rounded to retuse, midvein flat above, raised below, to 2 mm wide at the base, narrowing toward the apex, with dense, semiappressed, whitish to light yellowish trichomes c. 0.1 mm long, glabrescent, venation semicraspedodromous, with 5–9 secondary veins per side, 2-3 originating from the base, raised above, more so below, tertiary venation reticulate, distinctly

visible; petiole short, 1–2 mm long, c. 2 mm in diam., darker brown than the lamina, with dense, semi-appressed, yellowish to pale brown trichomes c. 0.1 mm long, glabrescent. Male and female flowers not seen. Fruits axillary, solitary, pedicel in fruit 5-11 mm long, 2 mm in diam. (to 3 mm in diam. distally), yellowish, covered with dense, appressed, pale yellow to whitish trichomes 0.1 mm long; fruiting calyx strongly accrescent, the base forming a short collar c.  $2-4 \times 3-4$  mm, slightly quadrangular, 3-4-lobed, the lobes  $9-15 \times 6-8$  mm, oblong, spreading to reflexed, adaxially convex, the surfaces discolorous in sicco, sparsely covered on both surfaces with appressed, whitish to light yellowish trichomes c. 0.2 mm long, glabrescent, margin weakly revolute, apex obtuse to rounded with distinct venation; fruit spherical to obloid or ovoid, 11–15 × 10–13 mm, minutely verrucose, green in vivo, with sparse, appressed, whitish to light yellow trichomes c. 0.2-0.4 mm long, glabrescent, apex apiculate. Seeds 4, 1 per locule, narrowly flattened ellipsoid,  $2.5-3 \times 0.9-1$  mm, weakly verrucose, dark brown to black.

Etymology. – The specific epithet refers to the fact that the color of the bark is grayish white, which is atypical for the genus and is expressed in its local name, 'Mapingo malandy' (= white *Diospyros*).

Vernacular names. – "Mapingo malandy" (Randrianaivo 3240).

Distribution and ecology. – Diospyros malandy is restricted to northern Madagascar, where it is known from two protected areas, Andrafiamena Andavokoera and Ankarana. It occurs in dry, semi-deciduous forest on tsingy, dry forest on basaltic soil, and dense, dry, degraded forest on reddish sand, as well as river banks, from c. 90 to 320 m elevation.

*Phenology.* – Flowering material of *Diospyros malandy* has been collected in February, and immature fruits have been collected in December.

Conservation status. – Diospyros malandy has a geographic range in the form of an Extent of Occurrence of 15 km² and a minimum Area of Occupancy of 15 km². It is present in two protected areas, Andrafiamena Andavokoera and Ankarana. It is also present along the roadside in the buffer zone of the Ankarana protected area, where it is threatened by forest clearing for agriculture, charcoal production, fire, and exploitation for firewood and house construction material, all of which will result in continuing decline. With respect to the most serious plausible threat of exploitation for firewood and house construction material, it exists at four locations. Therefore, D. malandy can be assessed for its risk of extinction as "Endangered" [EN B1ab(i,ii,iii,iv,v)+2ab(i,ii,iiii,iv,v)].



**Fig. 11.** – *Diospyros lowryi* G.E. Schatz. **A.** Branch in fruit; **B.** Fruit; **C.** Detail of leaf (adaxial surface). [A–C: *Schatz & Lowry 2617*, P] [Drawing: Alain Jouy]

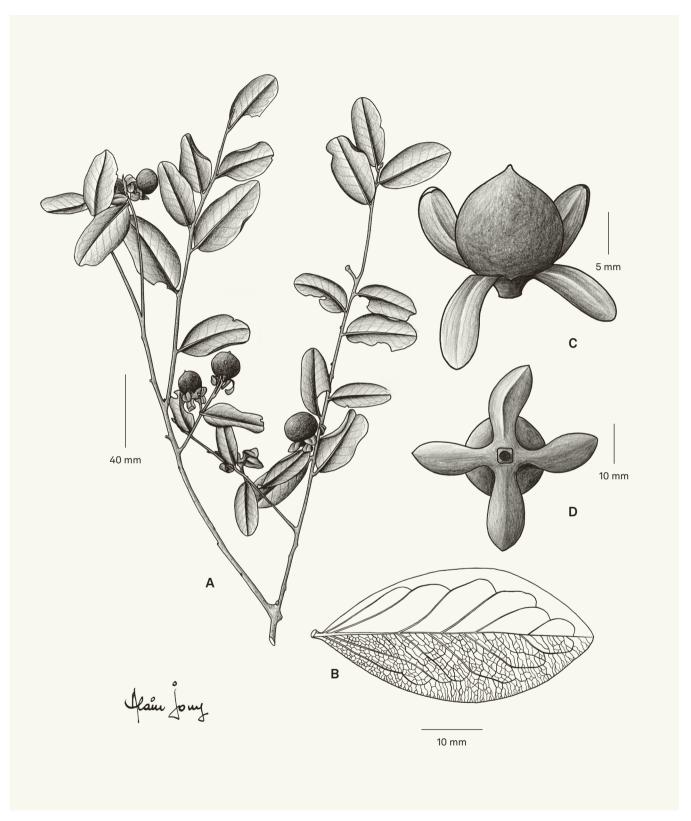


Fig. 12. – Diospyros malandy H.N. Rakouth, R. Randrianaivo, G.E. Schatz & Lowry. A. Branch in fruit; B. Detail of leaf (adaxial surface); C. Fruit; D. Fruiting calyx (seen from below).

[A: Bardot-Vaucoulon et al. 1316, P; B—D: Bardot-Vaucoulon et al. 1186] [Drawing: Alain Jouy]



Fig. 13. – Photographs of *Diospyros* L. species. A. *Diospyros malandy* H.N. Rakouth, R. Randrianaivo, G.E. Schatz & Lowry, branch with immature fruit; B. *Diospyros mimusops* G.E. Schatz & Lowry, branch with fruit; C–E. *Diospyros rakotovaoi* G.E. Schatz & Lowry: C. Branch with fruit; D–E. Male flowers.

[A: Randrianaivo 3240; B: Razakamalala 8563; C: Razakamalala et al. 3190; D–E: Razafitsalama 1141] [Photos: A: R. Randrianaivo; B: S. Andrianarivelo; C: C. Rakotovao; D–E: J. Razafitsalama]

Notes. – Diospyros malandy belongs to the Sclerophylla group (see notes under *D. bardotiae* for a list of its diagnostic features), within which it can be distinguished by its small fruits with a strongly accrescent, reflexed calyx, and leaves in dried material that have evident, densely reticulate tertiary venation and are usually light grayish to pale olive green above (often appearing matte to nearly glaucous), with a cuneate to rounded base, margin that is slightly revolute and undulate, and rounded to retuse apex.

Additional specimens examined. – MADAGASCAR. Reg. Diana [Prov. Antsiranana]: Ankarana, 14.I.2003, fr., Bardot-Vaucoulon 1186 (K, MO, P, TAN); ibid. loco, 25.I.2003, fr., Bardot-Vaucoulon 1316 (K MO, P, TAN); Ampondrabe, 12.II.2006, & fl., Rakotondrajaona 387 (CNARP, MO, P, TAN);

Ankarana, 146 m, 17.I.2014, ster., Randrianaivo 2406 (BR, DBEV, G, MO, P); Sajoavato, Sahafary, 25.I.2014, ster., Randrianaivo 2460 (BR, DBEV, G, MO, P); Sahafary, 25.I.2014, ster., Randrianaivo 2462 (BR, DBEV, G, MO, P); Sahafary, 25.I.2014, ster., Randrianaivo 2462 (BR, DBEV, G, MO, P); ibid. loco, 8.X.2018, ster., Randrianaivo et al. 3263 (DBEV, MO, P, TAN); ibid. loco, ster., Randrianaivo et al. 3264 (DBEV, G. MO, P); ibid. loco, ster., Randrianaivo et al. 3265 (DBEV, G, P); ibid. loco, 9.X.2018, y.fr., Randrianaivo et al. 3275 (DBEV, G, MO, P, TAN); Mahamasina, Ankarana, 9.X.2018, y.fr., Randrianaivo et al. 3276 (DBEV, G, MO, P, TAN); Ankarana, 22.III.2020, ster., Ravaoherinavalona et al. 118 (DBEV, MO, P, TAN); ibid. loco, ster., Ravaoherinavalona et al. 137 (DBEV, MO, P, TAN); ibid. loco, ster., Ravaoherinavalona et al. 138 (DBEV, MO, P, TAN); ibid. loco, ster., Ravaoherinavalona et al. 138 (DBEV, MO, P, TAN); ibid. loco, ster., Ravaoherinavalona et al. 139 (DBEV, MO, P, TAN); ibid. loco, 26.III.2020, ster., Ravaoherinavalona et al. 144 (DBEV, MO, P, TAN).

*Diospyros melanocarpa* G.E. Schatz & Lowry, **sp. nov.** (Fig. 14).

Holotypus: Madagascar. Reg. Analanjirofo [Prov. Toamasina]: Farankaraina, 19.IX.1957, fr., *Service Forestier 18343* (MO-6956008!; iso-: G [G00341738]!, K!, P [P00722678, P03829465]!, TEF [TEF000891]!).

Diospyros melanocarpa G.E. Schatz & Lowry resembles other members of the Decaryana group in having male flowers borne in cymose inflorescences and 1–3 axillary, short pedicellate fruits with an urceolate calyx and broadly triangular calyx lobes with revolute margins and a reflexed apex, but is distinguished by having shiny, glabrous, black fruits and small leaves [1.5–6.5(–8.7) × 0.8–4 cm].

Tree 15-20 tall, 30 cm DBH. Young stems terete, sparsely covered with very short, appressed and erect, whitish to golden trichomes c. 0.3 mm long, and an irregular, white, crystal-like, waxy substance (perhaps an artifact of drying), also sometimes present on leaves, pedicels, and fruits. Leaves pseudodistichous, lamina  $1.5-6.5(-8.7) \times 0.8-4$  cm, elliptic to rarely slightly obovate, chartaceous, glabrous above, initially rather densely covered with very short, appressed, white trichomes c. 0.3–0.4 mm long below, more densely so along the midvein, glabrescent, base cuneate, margin slightly revolute, apex acute to rounded, midvein flat to slightly impressed above, slightly raised at the base to flat at the apex below, venation weakly brochidodromous, with c. 7 secondary veins per side, mostly indistinct above, flat and indistinct below, tertiary venation finely reticulate; petiole 4-6 mm long, 1 mm in diam., canaliculate, sparsely covered with erect, white trichomes c. 0.3 mm long. Male flowers in axillary cymose inflorescences, 2-15 flowers per inflorescence, to 6 mm long, axes 0.5 mm in diam., rather densely covered with appressed, light golden trichomes c. 0.1-0.2 mm long, pedicel c. 1 mm long, 0.1 mm in diam., rather densely covered with appressed, light golden trichomes c. 0.2-0.3 mm long; calyx obconical, square in cross-section,  $2-2.5 \times 2$  mm, 4-lobed, triangular (1 × 1 mm), with moderately appressed, light golden trichomes 0.3-0.5 mm long outside, glabrous inside; corolla narrowly obconic, square in cross-section, 4.5 × 2.5 mm, 4-lobed, the lobes broadly ovate to triangular, 1 × 1 mm, densely covered with appressed, light golden trichomes to 1 mm long on the outside of the lobes and extending downward along the 4 corners, the rest of corolla glabrous outside, glabrous inside except for a tuft of trichomes at the apex of the lobes; stamens 12, inserted on the corolla at two levels 1/3 and 2/3 of the way up the corolla; filaments 0.5 mm long; anthers 0.8 mm long, ovoid; pistillode present, hemispherical, 0.5 mm long, glabrous, black in sicco. Female flowers not seen. Fruits 1-3 in axils of leaves or fallen leaves, sessile or pedicel in fruit c. 1–2 mm long, subtended by several bracteoles; fruiting calyx urceolate, 4 mm long, 4 mm in diam. at base, to 7-9 mm in diam. at the apex, 4-5-lobed, the

lobes  $4-5 \times 5-6$  mm, broadly triangular, densely covered with appressed, whitish gray trichomes c. 0.2–0.5 mm long, margins strongly revolute, apex strongly reflexed; fruit depressed ellipsoid-oblongoid to depressed spherical,  $12-15 \times 9-14$  mm, drying black, initially rather densely covered with semi-appressed, whitish golden trichomes c. 0.5–1.3 mm long, glabrescent, crowned by the style/stigma remnant, 1–2 mm long. Seeds 4–5, spherical wedge-shaped,  $13-14 \times 4-5$  mm, glabrous, black, shiny.

*Etymology.* – This specific epithet refers to the black color of the fruits.

Distribution and ecology. – Diospyros melanocarpa occurs primarily in northeastern Madagascar, from the area around the Baie d'Antongil north to Anjambalava-Ambavala situated to the north of Sambava, with a single collection from Tampolo (Madagascar Catalogue, 2021). It is found in low- to mid-elevation humid forest.

*Phenology.* – Flowering material has been collected in October, and collections with fruits have been collected in April, May, September, and October.

Conservation status. – Diospyros melanocarpa has a geographic range in the form of an Extent of Occurrence of 17,047 km² and a minimum Area of Occupancy of 28 km². It is present in three protected areas, Makirovana, Masoala, and Tampolo. Outside of the protected areas and also at Tampolo, it is threatened by forest clearing for agriculture, fire, and exploitation for firewood and house construction material, all of which will result in continuing decline. With respect to the most serious plausible threat of exploitation for firewood and house construction material, D. melanocarpa exists at seven locations, and was recently assessed for its risk of extinction as "Vulnerable" [VU B1ab(i,ii,iii,iv,v)+2ab(i,ii,iii,iv,v)] (IUCN, 2021).

Notes. – Diospyros melanocarpa is a member of the Decaryana group, characterized by male flowers borne in axillary, cymose inflorescences, short pedicellate female flowers borne in 1–3-flowered axillary fascicles, and depressed spherical fruit with an urceolate calyx and broadly ovate to triangular calyx lobes, the margins revolute and the apex reflexed. Other members of the group include *D. bezofensis* H. Perrier, *D. decaryana* H. Perrier, *D. decaryoides* G.E. Schatz & Lowry, and *D. implexicalyx* H. Perrier, as well as two new species that remain to be described. Within the Decaryana group, *D. melanocarpa* is the only species with shiny, glabrous, black fruits, and can also be distinguished by its small leaves (1.5–6.5(–8.7) × 0.8–4 cm), a feature shared only with *D. implexicalyx*.



Fig. 14. – Diospyros melanocarpa G.E. Schatz & Lowry. A. Branch in fruit; B. Fruit; C. Fruit (seen from above); D. Detail of leaf (adaxial surface). [A—D: Service Forestier 18343, P] [Drawing: Alain Jouy]

Additional specimens examined. – MADAGASCAR. Reg. Analanjirofo [Prov. Toamasina]: Tampolo, 11.X.2001, y.fr., Rabevohitra et al. 3869 (MO, P, TAN, WAG). Reg. SAVA [Prov. Antsiranana]: Ranovery, 26.X.2010, & fl., Bernard & Ndrano 1695 (MO, P, TAN); Mt. Anjenabe, 3–7.XI.1950, fr., Humbert & Capuron 18343 (P); Nosiarina, 7.V.2000, y.fr., Rabenantoandro et al. 208 (MO, P, TAN); Tsihomanaomby, 13.I.2021, fr., C. Rakotonirina & Martial 663 (DBEV, MO, P, TAN); ibid loc., 12.XII.2020, y.fr., Razakamalala et al. 8821 (MO, P, TAN); massif de l'Anjenabe, 7.IX.1950, fr., Service Forestier 770 (G, K, MO, P [P03829464], TEF, W); Andrapengy, 11.IV.1967, y.fr., Service Forestier 27763 (G, MO, P, TEF); Cap-Est, 19–21.IV.1967, fr., Service Forestier 27763 (G, MO, P, TEF).

*Diospyros mimusops* G.E. Schatz & Lowry, **sp. nov.** (Fig. 13B, 15).

Holotypus: Madagascar. Reg. Anosy [Prov. Toliara]: Antsotso, 24.V.2006, fr., *Antilahimena et al. 4887* (MO-6336318!; iso-: P [P06490534]!, TAN [TAN002011]!, TEF!).

Diospyros mimusops G.E. Schatz & Lowry resembles other members of the Tetraclis group in having leaves with a mucronate apex, male flowers borne in cymose inflorescences, and often valvate corolla aestivation, but is distinguished by having glabrous and sometimes glaucous young stems and leaves.

Tree 5-20 m tall, 8-17 cm DBH. Young stems terete to flattened, glabrous, sometimes glaucous in sicco. Leaves distichous, lamina 6–11.5 × 2.2–4.2 cm, elliptic to obovate, coriaceous, glabrous, sometimes shiny or glaucous above in sicco, base attenuate to acute, margin revolute, apex acute to shortly acuminate, occasionally rounded to retuse, acumen 2-3 mm long, usually with a very short, black mucron, midvein slightly impressed above, raised below, venation weakly brochidodromous, loops of secondaries \(\frac{1}{4}\)-\(\frac{1}{3}\) in from margin, with 10-15 secondary veins per side, slightly raised on both surfaces, tertiary venation densely reticulate, raised and evident above and below; petiole 12-22 mm long, 1-1.5 mm in diam., glabrous. Male flowers borne in axillary, 3-5-flowered cymes, 1 inflorescence per axil, peduncle 10-20 mm long, 0.5-1 mm in diam., sparsely covered with appressed, white trichomes c. 0.2 mm long, pedicel 5–13 mm long, 0.5–0.8 mm in diam., rather sparsely covered with appressed, white trichomes c. 0.2 mm long; calyx obconic,  $4-5 \times 5-6$  mm, 4-lobed, the lobes broadly triangular,  $2.5 \times 3.5$  mm, apex shortly acuminate, rather sparsely covered outside with appressed, white trichomes c. 0.2 mm long, glabrous inside; corolla tubular, 10.5 × 6 mm, 4-lobed, the lobes valvate, 3.5 × 3 mm, triangular, rather sparsely covered with appressed, white trichomes c. 0.2 mm long on both surfaces; stamens c. 30, sparsely covered throughout with appressed, white trichomes c. 0.2 mm long, of variable lengths, inserted on the corolla at the midpoint, lower series with slender, terete, sigmoid filaments c. 1.5 mm long, upper series with flattened filaments 3.5 mm long, anthers 2.5 mm long, lanceolate, apex

acuminate, dehiscing by apical pores; pistillode absent. *Female flowers* not seen. *Fruits* axillary, solitary, pedicel in fruit 4–5 mm long, 4–5 mm in diam., sparsely covered with appressed, white trichomes c. 0.2 mm long; fruiting calyx broadly cupuliform, 7 × 18–22 mm, with a distinct basal collar c. 2 mm long, 6–7 mm in diam., (3–)4-lobed, sometimes very shallowly so with nearly indistinct lobes, the lobes broadly triangular, 2–9 × 10–18 mm, margin flat or revolute, sparsely covered with appressed, white trichomes c. 0.2 mm long, glabrescent; fruit depressed spherical, 16–28 × 17–32 mm, crowned with a very short style/stigma remnant, sparsely covered with appressed, white trichomes c. 0.2 mm long. *Seeds* 4, spherical wedge-shaped, 23 × 17 mm, glabrous.

Etymology. – The specific epithet refers to the fact that the vegetative features of this species superficially resemble those of some species of the genus *Mimusops* L. (*Sapotaceae*).

Distribution and ecology. – Diospyros mimusops is known from the Bemangidy forest near Iaboakoho on the eastern slope of the Vohimena mountains and from near the Col de Maningotry in Parcel 1 of Andohahela National Park (Madagascar Catalogue, 2021). It occurs in low- and midelevation humid forest.

*Phenology.* – Flowering material has been collected in December, and collections with fruit have been made in April, May, and November.

Conservation status. – Diospyros mimusops has a very restricted geographic range in the form of an Extent of Occurrence of 12 km² and an Area of Occupancy of 12 km². Its distribution is wholly contained within the protected areas of Andohahela and Tsitongambarika. Nevertheless, it occurs near the edge of the forest at Iaboakoho and is thus threatened by ongoing exploitation of trees for firewood and house construction material, which will result in continuing decline of quality of habitat and mature individuals. With respect to the most serious plausible threat of exploitation of trees for firewood and house construction material, *D. mimusops* exists at two locations, and was recently assessed for its risk of extinction as "Endangered" [EN B1ab(iii,v)+2ab(iii,v)] (IUCN, 2021).

Notes. – Diospyros mimusops is a member of the Tetraclis group (see notes under *D. ambanjensis* for a list of its diagnostic features), and along with *D. beberonnii* (see above), is the only member found in far southern Madagascar. Within the group, *D. mimusops* can be distinguished by its glabrous and sometimes glaucous young stems and leaves.

Additional specimens examined. – MADAGASCAR. Reg. Anosy [Prov. Toliara]: road towards Ranomafana Sud, 5.XII.1989, & fl., McPherson 14621 (G, MO, P, TAN); Antsotso, 2.IV.2008, fr., Rabenantoandro et al. 1911



Fig. 15. – Diospyros mimusops G.E. Schatz & Lowry. A. Branch with fruit; B. Branch with male inflorescences; C. Detail of leaf (abaxial surface); D. Schematic section of male flower; E. Fruit.

[A, C, E: Antilahimena et al. 4887, P; B, D: McPherson 14621, P] [Drawing: Alain Jouy]

(MO, P, TAN); *ibid. loco*, 22.V.2006, fr., *Randriatafika et al. 676* (MO, P, TAN); 8.XII.2007, ♂ fl., *Razakamalala et al. 3771* (MO, P, TAN); *ibid. loco*, 1.IV.2014, ster., *Razakamalala 7737* (MO, P, TAN); *ibid. loco*, 11.II. 2019, ster., *Razakamalala et al. 8285*, *8286*, *8289* (DBEV, G, MO, P, TAN); Antanitsara, 5.XI.2019, y.fr., *Razakamalala & Andrianarivelo 8563* (DBEV, MO, P, TAN).

*Diospyros quadrangularis* G.E. Schatz & Lowry, **sp. nov.** (Fig. 16).

Holotypus: Madagascar. Reg. Analanjirofo [Prov. Toamasina]: Ambinanitelo, 9.IX.2004, fr., *Antilahimena* 2876 (MO-6336086!; iso-: P [P03975182]!, TAN!).

Diospyros quadrangularis G.E. Schatz & Lowry resembles other members of the Subsessilifolia group in having flattened young stems and leaves with a short petiole and a rounded to cordate base, but is distinguished by having young stems that are 4-angled and square in cross section, and relatively large fruits (40–60 × 40–53 mm).

Tree 4-12 m tall, 10-20 cm DBH. Young stems distinctly 4-angled, square in cross-section, glabrous to rarely very sparsely covered with minute (< 0.1 mm long), appressed trichomes, initially reddish brown becoming white with age. Leaves distichous, lamina 3–13.7 × 1.4–7.8 cm, narrowly obovate to broadly elliptic, chartaceous to subcoriaceous, glabrous on both surfaces, base rounded to subcordate to cordate, rarely obtuse, margin flat, apex acute to rounded, midvein slightly impressed above, prominently raised below, distinctly narrowing from base to apex, venation brochidodromous, with 7-10 secondary veins per side, flat to slightly raised above and below, tertiary venation indistinct; petiole 1–5 mm long, 1–2 mm in diam., glabrous. Male and female flowers not seen. Fruits axillary, solitary, pedicel in fruit 1–7 mm long, 5–9 mm in diam., densely covered with semi-appressed, golden brown trichomes 0.5 mm long, pedicel scar 6-10 mm in diam.; calyx in fruit cupuliform to broadly cupuliform, 10-12 × 24-32 mm, 4-lobed, the lobes broadly triangular, 4-10 × 16-20 mm, densely covered with semi-appressed, golden brown trichomes 0.5 mm long on both surfaces, margins flat; fruit spherical to slightly ellipsoid, 40-60 × 40-53 mm, glabrous except very sparsely covered with appressed golden trichomes c. 0.5 mm long at the base where the fruit is covered by the calyx. Seeds 6-8, spherical wedgeshaped, 30–33 × 14–15 mm, glabrous, reddish brown, slightly shiny.

*Etymology.* – This specific epithet refers to the fact that the young stems are 4-angled.

Vernacular names. – "Fandramanan'ala" (Razanatsima 127), "Hazomainty" (Service Forestier 15101).

Distribution and ecology. – Diospyros quadrangularis occurs in northeastern Madagascar, from Tampolo north to

Ambondrobe, with outlier subpopulations farther south at Ambalabe in the Corridor Ankeniheny-Zahamena protected area, and farther north at Andrafiamena (MADAGASCAR CATALOGUE, 2021). It is found in low- and mid-elevation humid forest.

*Phenology.* – Fruiting material has been collected in March, and from May to November.

Conservation status. – Diospyros quadrangularis has a geographic range in the form of an Extent of Occurrence of 54,568 km² and a minimum Area of Occupancy of 60 km². It is present in seven protected areas, i.e., Andrafiamena Andavokoera, Anjanaharibe-Sud, Corridor Ankeniheny-Zahamena (Ambalabe), COMATSA Sud, Makira, Makirovana-Tsihomanaomby, and Masoala. Outside of protected areas, it is threatened by forest clearing for agriculture, fire, and exploitation for firewood and house construction material, all of which will result in continuing decline. With respect to the most serious plausible threat of forest clearing for agriculture, it exists at 12 locations. Therefore, D. quadrangularis can be assessed for its risk of extinction as "Near Threatened" [NT], as it is close to qualifying for VU status under criterion B2.

Notes. – Diospyros quadrangularis is a member of the Subsessilifolia group, characterized by flattened young stems and leaves with a short petiole and a rounded to cordate base. Other members of the group include *D. mangabensis* Aug. DC., *D. mangorensis* H. Perrier, *D. sphaerosepala*, and *D. subsessilifolia* H. Perrier, as well as more than a dozen new species awaiting description. Within the Subsessilifolia group, *D. quadrangularis* can be distinguished by its 4-angled young stems that are square in cross section, and relatively large fruits (40–60 × 40–53 mm).

Additional specimens examined. - MADAGASCAR. Reg. Analanjirofo [Prov. Toamasina]: Anjahana, 19. VII. 2002, v.fr., Antilahimena et al. 1214 (MO, P, TAN); Tampolo, 18. VIII. 1955, fr., Service Forestier 15101 (MO, P, TEF); ibid. loco, 23.I.2014, ster., Razakamalala & Bernard 7710 (BR, G, MO, P, TAN); Île Ste. Marie, 18.XII.2017, y.fr., Razakamalala 8186 (MO, P, TAN); ibid. loco et datum, Razakamalala 8188 (MO, P, TAN); Ambohitsitondroina de Mahalevona, 29.XI.1953, fr., Service Forestier 8690 (MO, P, TEF); Tampolo, 28–29.VIII.1957, fr., Service Forestier 18154 (MO, P, TEF); Île Sainte-Marie, 16.V.1969, fr., Service Forestier 28806 (MO, P, TEF); ibid. loco, 16. V.1969, y.fr., Service Forestier 28819 (G, MO, P, TEF). Reg. Atsinanana [Prov. Toamasina]: Ambalabe, 12.VI.2006, fr., Razanatsima 127 (G, MO, P, TAN); ibid. loco, 5.V.2010, y.fr., Razanatsima 885 (MO, P, TAN); ibid. loco, 12.VII.2017, y.fr., Razanatsima et al. 1753 (MO, P, TAN). Reg. SAVA [Prov. Antsiranana]: Anjanaharibe-Sud Reserve, 7.IX.1997, fr., Birkinshaw et al. 486 (MO, P, TAN); Antsirabe-Nord, Andavanambo, Tsihomanaomby, access from Antanambaonisokitra, 23.IV.2014, y.fr., Birkinshaw et al. 2013 (MO, P, TAN); Anjahankely, 18.XI.2010, fr., Burivalova 33 (G, MO, P, TAN); massif d'Antsahabe, 14.X.2004, fr., Callmander et al. 220 (G, MO, P, TAN); Amdisatrana, 2. VIII. 1997, fr., McPherson 17178 (MO, P, TAN); Antranohofa, 9.V.1998, v.fr., Ravelonarivo 1094 (MO, P, TAN); Manakana, 13.III.2004,

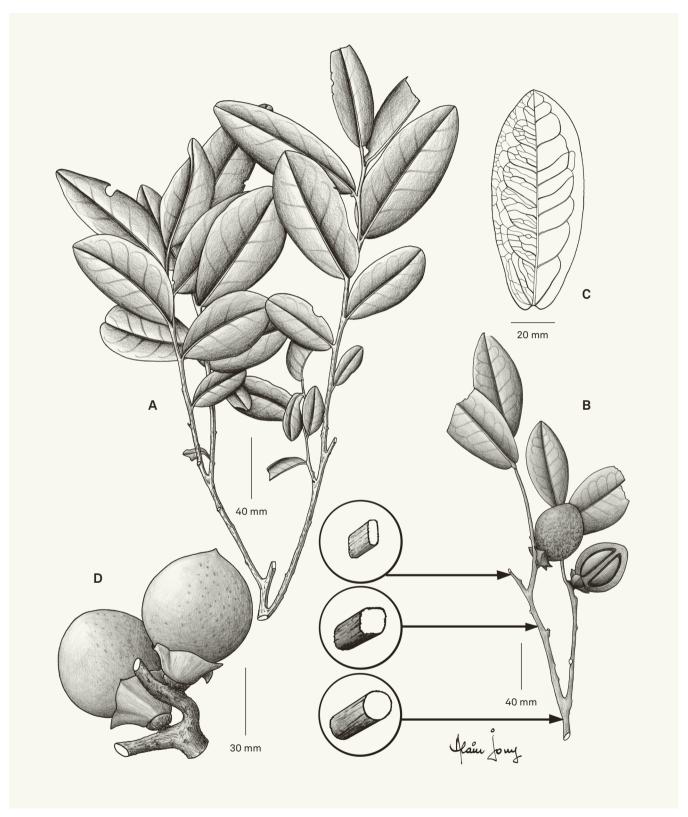


Fig. 16. – Diospyros quadrangularis G.E. Schatz & Lowry. A. Branch; B. Fruiting branch with stem cross-sections; C. Detail of leaf (adaxial surface); D. Fruits.

[A: Birkinshaw et al. 486, P; B—D: Antilahimena 2876, P] [Drawing: Alain Jouy]

fr., Razakamalala et al. 1016 (G, MO, P, TAN); ibid. loco, 20.V.2004, fr., Razakamalala 1346 (G, MO, P, TAN).

*Diospyros rakotovaoi* G.E. Schatz & Lowry, **sp. nov.** (Fig. 13C-E, 17).

Holotypus: MADAGASCAR. Reg. SAVA [Prov. Antsiranana]: Antsahaberaoka, 21.II.2007, fr., *Rakotovao et al. 3692* (MO-6214314!; iso-: G!, P [P04539975]!, TAN [TAN002010]!).

Diospyros rakotovaoi G.E. Schatz & Lowry resembles other members of the Tetraclis group in having fauve to rusty indumentum, leaves generally with a mucronate apex, male flowers borne in cymose inflorescences, and often valvate corolla aestivation, but is distinguished by its obovate leaves that are glabrous and shiny above and densely covered with semi-erect light brown trichomes along the midvein and secondary veins below, rendering it somewhat scabrous, and its relatively large spherical fruit 29–37 mm in diam., densely covered with erect, rusty brown trichomes 0.3 mm long.

Tree 6-25 m tall, 6-15 cm DBH. Young stems terete, densely covered with slightly curly, erect, light brown trichomes 0.5 mm long, distinctly lenticellate. Leaves distichous, lamina  $6.5-11.5 \times 2.3-3.7$  cm, obovate, chartaceous to subcoriaceous, glabrous, shiny above, densely covered with semi-erect, whitish trichomes c. 1 mm long along the midvein and secondary veins, and sparsely covered with semi-erect light brown trichomes c. 0.5 mm long elsewhere below, somewhat scabrous, glabrescent, base attenuate to cuneate, margin flat, apex rounded, rarely somewhat retuse, with a distinct mucron c. 1 mm long, midvein impressed above, prominently raised below, venation brochidodromous, with 7-9 secondary veins per side, flat above, raised below, tertiary venation reticulate, flat above, slightly raised below; petiole 5-9 mm long, 1 mm in diam., densely covered with slightly curly, erect, light brown trichomes 0.5 mm long, glabrescent. Male flowers in cymose, axillary inflorescences, each with 7 flowers; inflorescence 15-20 mm long, the axes densely covered with erect, rusty brown trichomes 0.3 mm long, pedicel 3–13 mm long, 1.5 mm in diam.; calyx cupuliform, 5 × 8 mm, 1 mm thick, densely covered outside with erect, rusty brown trichomes 0.3 mm long, glabrous inside except for a ring of very short trichomes at the base, 4-lobed,  $4 \times 5$  mm, broadly triangular; corolla cylindrical, 8 × 7 mm, 1 mm thick, densely covered with appressed, light brown trichomes 0.2 mm long on both surfaces, 4-lobed, the lobes valvate, 4.5 × 4.5 mm, triangular; stamens 8, inserted in a single whorl on the corolla c. 1/3 from the base, filaments 3 mm long, with a small hook-like basal appendage, densely covered with appressed, light brown trichomes 0.5–0.7 mm long, anthers 3 mm long, lanceolate, apex apiculate, dehiscing by apical pores; torus with a ring 3 mm in diam. of dense, erect trichomes 1 mm long; pistillode absent.

Female flowers not seen. Fruits axillary, solitary, pedicel in fruit 4 mm long, 4 mm in diam., densely covered with erect, rusty brown trichomes 0.3 mm long; fruiting calyx broadly cupuliform, 10–12 × 25–27 mm, 4-lobed, the lobes broadly triangular, 10–12 × 17–19 mm, margin flat to slightly revolute, densely covered with erect, rusty brown trichomes 0.3 mm long; fruit spherical, 29–37 mm in diam., densely covered with erect, rusty brown trichomes 0.3 mm long. Seeds 1–4, ovoid, 17 mm long, 10 mm in diam., black, matte.

Etymology. – This species honors our friend and colleague Charles Rakotovao, one of Madagascar's most prolific field botanists, who has made more than 8500 collections starting in 1994, including 200 numbers of *Diospyros*, contributing immensely to our knowledge of the Malagasy flora. Since joining the staff of the Missouri Botanical Garden in 2005, Charles has conducted field work throughout the island and has taken more than 4100 excellent photos (Madagascar Catalogue, 2021), documenting both his own collections and those of many colleagues.

Distribution and ecology. – Disspyros rakotovaoi occurs in the mountains of northern Madagascar, from the Anjanaharibe-Sud reserve north to Antsahabe in the Daraina region, and extending into the Sambirano region in the northwestern part of the island at the Galoko-Kalobinono and Tsaratanana protected areas (Madagascar Catalogue, 2021), where it is found in mid- to high-elevation humid to subhumid forest.

*Phenology.* – Flowering material has been collected in November, and specimens with fruit have been made in February, May, August, and November.

Conservation status. - Diospyros rakotovaoi has a restricted geographic range in the form of an Extent of Occurrence of 12,793 km<sup>2</sup> and a minimum Area of Occupancy of 28 km<sup>2</sup>. Its distribution is wholly contained within six protected areas, i.e., Anjanaharibe-Sud, COMATSA Nord, Galoko-Kalobinono, Loky Manambato, Makirovana, and Tsaratanana. Nevertheless, at several localities it has been collected at the forest edge where there are active threats consisting of forest clearing for agriculture, fire, and exploitation of trees for firewood and house construction material, which will result in continuing decline of quality of habitat and mature individuals. With respect to the most serious plausible threat of exploitation of trees for firewood and house construction material, D. rakotovaoi exists at seven locations, and was recently assessed for its risk of extinction as "Vulnerable" [VU B1ab(iii,v)+2ab(iii,v)] (IUCN, 2021).

Notes. - Diospyros rakotovaoi is another member of the Tetraclis group (see notes under *D. ambanjensis* for a list of its

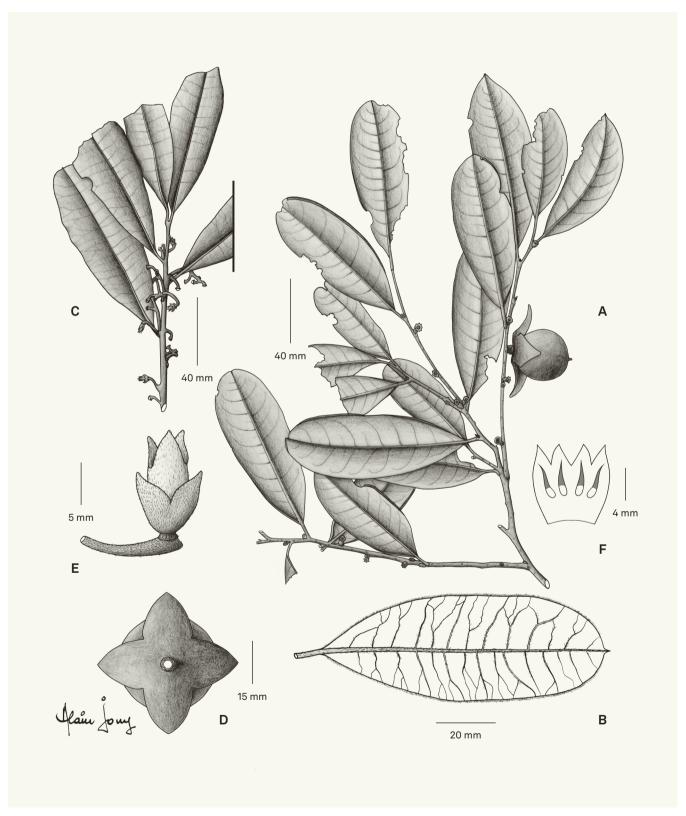


Fig. 17. – Diospyros rakotovaoi G.E. Schatz & Lowry. A. Branch with fruits; B. Detail of leaf (abaxial surface); C. Branch with male inflorescences; D. Fruiting calyx (seen from below); E. Male flower; F. Schematic section of male flower.

[A, B, D: Raharimampionona et al. 303, P; C, E, F: Razafitsalama 1141, P] [Drawing: Alain Jouy]

diagnostic characters), within which it is characterized by its leaves with an obovate lamina with a glabrous, shiny adaxial surface and the abaxial surface densely covered with semi-erect, light brown trichomes along the midvein and secondary veins, rendering it somewhat scabrous, as well as its relatively large spherical fruits (29–37 mm in diam.) that are densely covered with erect, rusty brown trichomes 0.3 mm long.

Additional specimens examined. – MADAGASCAR. Reg. Diana [Prov. Antsiranana]: Réserve Intégrale de Tsaratanana, 31.VIII.2000, fr., Antilahimena 596 (MO, P, TAN); Kalebenono, 25.XI.2006, ♂ fl., Razafitsalama ℰ Torze 1141 (MO, P, TAN). Reg. SAVA [Prov. Antsiranana]: forêt d'Antsahabe, 26.XI.2004, ♂ fl., Gautier 4755 (G, MO, P, TAN); Belalona, 25.V.2009, fr., Raharimampionona et al. 303 (MO, P, TAN, TEF); Réserve Spéciale d'Anjanaharibe-Sud, 9.XI.1999, fr., Rakotomalaza ℰ Ravelomanantsoa 2145 (G); ibid. loco, 3.XI.1994, fr., Ravelonarivo ℰ Rabesonina 508 (L, MO, P, TAN, WAG); Tsaratanana, 6.II.2006, fr., Razakamalala et al. 3190 (G, MO, P, TAN).

*Diospyros taikintana* G.E. Schatz & Lowry, **sp. nov.** (Fig. 18).

Holotypus: Madagascar. Reg. Sofia [Prov. Mahajanga]: Ambohimirahavavy, 19.I−12.II.1951, ♀ fl., *Humbert & Capuron 24919* (MO-6956011!; iso-: G [G00341739]!, K!, P [P00580401, P03829461]!, TAN!, US!, W!).

Diospyros taikintana G.E. Schatz & Lowry resembles other members of the Squamosa group in having leaves with the midvein impressed adaxially and female flowers enclosed within multiple distichous, overlapping, scale-like bracts in bud, but is distinguished by its small leaves (3–5.5 × 0.8–2.3 cm) with dense indumentum on the abaxial surface, often 3-merous female flowers, and squamose floral bracts that form a nearly spherical cluster around each bud.

Tree 18-25 m tall, 25-40 cm DBH. Bark thin (5 mm), nearly entirely black. Young stems terete, dark brown to blackish, with numerous small lenticels, moderately densely covered with short, erect, straight to curly trichomes c. 1 mm long and/ or long, fauve, appressed trichomes c. 1 mm long, glabrescent. Leaves distichous, lamina 3-5.5 × 0.8-2.3 cm, narrowly ovate to elliptic or occasionally oblong, coriaceous, glossy above, initially with appressed trichomes c. 0.1 mm long, glabrescent, matte below, initially densely covered with white, silky, appressed trichomes to c. 1 mm long and rusty, appressed trichomes c. 0.1 mm long below, glabrescent, base obtuse to rounded, margin flat, apex acute to acuminate, midvein raised to slightly impressed above, glabrous or densely covered with white, curly, semi-appressed trichomes, raised below, venation weakly brochidodromous, with 6-9 secondary veins per side, indistinct to faintly visible and slightly raised above, slightly raised below; petiole 1-4 mm long, 0.7-1 mm in diam., terete to slightly flat-topped or canaliculate, densely covered with curly, semi-appressed, white to light golden trichomes 0.7 mm long and appressed, rusty trichomes 0.1 mm long, glabrescent. Male flowers not seen. Female flowers solitary, in the axils of

leaves, 3(-4)-merous, pedicel 1-2 mm long, 0.5 mm in diam., bearing 7-9 distichous, overlapping, cucullate, scale-like bracts enclosing the flower in bud, 1.5–5 × 1.5–6 mm, broadly elliptic to circular, cucullate, becoming progressively larger from the base to apex of the pedicel, densely covered outside with white and fauve, appressed trichomes, glabrous inside, the margins densely ciliate; sepals fused into a cupular calyx, 3-4 × 4.5 mm, apex truncate, without any evident lobes or sometimes with three or four groups of trichomes slightly exserted above the rim, densely covered outside with appressed, fauve trichomes, glabrous inside; fused corolla with short (1.5 mm) urceolate tube and 3-4 spreading lobes, cream white, lobes 3 × 3 mm, apex rounded, densely covered outside with fauve, appressed trichomes, glabrous inside; staminodia 9, inserted on the corolla tube just below the lobes; ovary ovoid, 2-3 mm long, style 1-2 mm long, with 3-5 flat-topped stigmatic branches. Fruits axillary, solitary, pedicel in fruit 1-1.5 mm, 2 mm in diam., glabrous, bearing numerous bract scars; fruiting calyx broadly cupuliform, 4-5 × 9-10 mm, 3-4-lobed, the lobes broadly triangular, 2 × 5 mm, margin revolute, the apex strongly reflexed, densely covered outside with a mixture of semi-appressed, blackish and dark brown trichomes 1-1.5 mm long, glabrous inside except with shorter trichomes apically along the rim and exposed surface of lobes, pedicel scar 2 mm in diam.; fruit spherical to slightly obloid, the apex slightly depressed,  $7.5-8.5 \times 7.5-9$  mm, glabrous, light brown, shiny, crowned by the persistent style/stigma, 1-1.3 mm long. Seeds 3-4, flattened ellipsoid, 6–7 × 4–5 mm, glabrous, black, shiny.

Etymology. – The species epithet is the Malagasy word for pill bugs, members of the isopod family Armadillidiidae, which, when rolled into a ball to assume a defensive posture, strongly resemble the squamose bracts that subtend the flower buds of *Diospyros taikintana*.

Distribution and ecology. – Diospyros taikintana is known from a single locality in the Ambohimirahavavy massif in the northern part of the island (Madagascar Catalogue, 2021), where it was collected in high-elevation subhumid to montane forest.

*Phenology.* – Flowering and fruiting material was collected in February.

Conservation status. – Diospyros taikintana has an extremely restricted geographic range in the form of an Area of Occupancy of 4 km². It is present only in the protected area of COMATSA Nord. Given the isolated and remote nature of its distribution, there are no known external threats. Therefore, D. taikintana can be assessed as "Least Concern" [LC], with the caveat that such a status is contingent upon the effective management of the COMATSA Nord protected area.

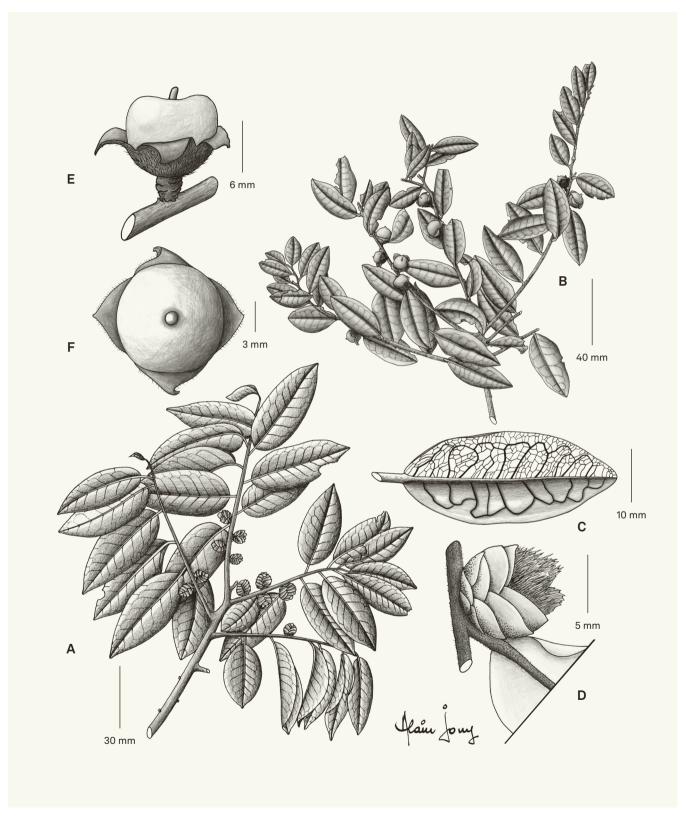


Fig. 18. – Diospyros taikintana G.E. Schatz & Lowry. A. Branch with flower buds; B. Branch with fruits; C. Detail of leaf venation (abaxial surface); D. Detail of flower bud with subtending bracts; E. Fruit (seen from side); F. Fruit (seen from above).

[A, D: Service Forestier 983, P; B—C, E—F: Service Forestier 988, P] [Drawing: Alain Jouy]

Notes. – Diospyros taikintana is possibly a member of the Squamosa group, which comprises nine species characterized by having leaves with the midvein impressed adaxially, and female buds and flowers enclosed within multiple distichous, overlapping, scale-like bracts (Schatz & Lowry, 2020). Within the Squamosa group, D. taikintana would be distinguished by its leaves with small lamina (3–5.5 × 0.8–2.3 cm) bearing dense indumentum on the abaxial surface, often 3-merous female flowers, and floral bracts that form a nearly spherical cluster around each bud.

We strongly suspect that the material of this species represents just two collections, one in flower comprising *Humbert & Capuron 24919* and *Service Forestier 983*, and the other in fruit, represented by *Humbert & Capuron 24927* and *Service Forestier 988*. Indeed, when Capuron was in the field with Humbert (and others, e.g. Leandri), he routinely reserved material of woody collections for the Service Forestier series, resulting in a single gathering entered into both Humbert's and the Service Forestier number series.

Additional specimens examined. – MADAGASCAR. Reg. Sofia [Prov. Mahajanga]: Ambohimirahavavy, 19.I–12.II.1951, fr., Humbert & Capuron 24927 (FHO, MO, P, TAN, WAG); ibid. loco, 5.II.1951, ♀ fl., Service Forestier 983 (G, MO, P [2 sheets], TEF); ibid. loco, 6.II.1951, fr., Service Forestier 988 (G, K, NY, P [2 sheets], TEF, US, W).

# **Acknowledgments**

We are grateful to Alain Jouy for the excellent illustrations and to the curators of the following herbaria for providing access to their collections: G, K, P, TAN, TEF, US. We thank the editorial team at Candollea, Joel Calvo and Martin Callmander, as well as an anonymous reviewer, for helpful comments on an earlier version of the manuscript. The Government of Madagascar (Ministère de l'Environnement et du Développement Durable) kindly provided the necessary authorization for conducting field work, and the Parc Botanique et Zoologique de Tsimbazaza assisted with the export of duplicate specimens. This work was supported by two generous grants provided by the Fondation Franklinia, one for our work on Diospyros and another in support of the conservation and sustainable management of Madagascar's precious woods. Field work and most of the other activities being conducted by the Madagascar Precious Woods Consortium as part of the G3D (Gestion Durable des bois précieux Dalbergia et Diospyros de Madagascar) Project were funded by the Délégation de l'Union Européenne à Madagascar (DEUM).

### References

GeoCAT (2020). Geospatial Conservation Assessment Tool. Royal Botanic Gardens, Kew. [http://geocat.kew.org]

- IUCN (2012). IUCN Red List Categories and Criteria: Version 3.1.
  Ed. 2. IUCN Species Survival Commission, Gland and Cambridge.
- IUCN (2021). The IUCN Red List of Threatened Species. [https://www.iucnredlist.org]
- Linan, A.G., G.E. Schatz & P.P. Lowry II (2021). Taxonomic studies of Diospyros (Ebenaceae) from the Malagasy region. VII. Revision of Diospyros section Forbesia in Madagascar and the Comoro islands. *Ann. Missouri Bot. Gard.* 106: 72–110. DOI: https://doi.org/10.3417/2021644
- MADAGASCAR CATALOGUE (2021). Catalogue of the Plants of Madagascar. Missouri Botanical Garden, St. Louis & Antananarivo. [http://www.tropicos.org/Project/Madagascar]
- MASON, J., M. PARKER, L. VARY, P.P. LOWRY II, S. HASSOLD & G. RUTA (2016). Malagasy precious hardwoods: Scientific and technical assessment to meet CITES objectives. Report submitted by the World Resources Institute and the World Bank. [https://www.scribd.com/document/318123493/WRI-WB-Malagasy-Precious-Woods-Assessment-1-pdf]
- Perrier de la Bâthie, H. (1952). Ebenacées. *In:* Humbert, H. (ed.), *Fl. Madagascar Comores* 165.
- Poncet, V., P. Birnbaum, V. Burtet-Sarramegna, A. de Kochko, B. Fogliani, G. Gâteblé, S. Isnard, T. Jaffré, D. Job, F. Munoz, J. Munzinger, C.P. Scutt, R. Tournebize, S. Trueba & Y. Pillon (2019). Amborella bearing witness to the past? *Ann. Plant Rev. Online* 2: 1–41. DOI: https://doi.org/10.1002/9781119312994.apr0689
- Schatz, G.E. & P.P. Lowry II (2011). Nomenclatural notes on Malagasy Diospyros L. (Ebenaceae). *Adansonia* ser. 3, 33: 271–281. DOI: https://doi.org/10.5252/a2011n2a1
- Schatz, G.E. & P.P. Lowry II (2018). Taxonomic studies of Diospyros L. (Ebenaceae) from the Malagasy Region. III. New species from the island of Nosy Mangabe in the Bay of Antongil. *Novon* 26: 272–286. DOI: https://doi.org/10.3417/2018209
- Schatz, G.E. & P.P. Lowry II (2020). Taxonomic studies of Diospyros L. (Ebenaceae) from the Malagasy region. IV. Synoptic revision of the Squamosa group in Madagascar and the Comoro Islands. *Adansonia* ser. 3, 42: 201–218. DOI: https://doi.org/10.5252/adansonia2020v42a10
- Schatz, G.E., P.P. Lowry II & P.B. Phillipson (2020). Taxonomic studies of Diospyros L. (Ebenaceae) from the Malagasy region. V. Synoptic revision of the Bernieriana group in Madagascar and the Comoro Islands. *Candollea* 75: 203–218. DOI: https://doi.org/10.15553/c2020v752a5
- Schatz, G.E., P.P. Lowry II & H.N. Rakouth (in press). Taxonomic studies of Diospyros L. (Ebenaceae) from the Malagasy region. VIII. New species from the humid littoral forest of eastern Madagascar. *Novon*.